LIFE-HISTORY PATTERNS OF NORTH AMERICAN ELK: EFFECTS OF POPULATION DENSITY ON RESOURCE PARTITIONING, REPRODUCTION, AND PLANT PRODUCTIVITY

A DISSERTATION

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

May 2004

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ABSTRACT

I examined density dependence in North American elk (*Cervus elaphus*) and effects of density dependent processes on resource partitioning, physical condition, reproduction, and ecosystem processes. Specifically, I examined spatial, temporal, and dietary niche partitioning among elk, mule deer (*Odocoileus hemionus*) and cattle (*Bos taurus*). I tested hypotheses related to density-dependent processes in elk by creating populations at high (20.1 elk / km^2) and low (4.1 elk / km^2) density. I hypothesized that physical condition and fecundity of females would be lower in an area of high population density than in the low-density area. Simultaneously, I tested hypotheses relating to herbivore optimization in response to varying levels of herbivory. I observed differences among elk, mule deer, and cattle in diets and use of space, particularly elevation, slope, and use of logged forest. Those 3 herbivores showed strong avoidance over a 6-h temporal window, but that effect was weaker for the previous 7 days. Changes in habitat use by elk and mule deer in response to addition and removal of cattle indicated competitive displacement. Results of the experiment to examine density dependence in elk indicated reduced physical condition and reproduction in the high-density population compared with low-density population. Pregnancy rates were most affected by body condition and mass of females. Density dependence in elk also had strong effects on plant communities; net aboveground primary productivity (NAPP) increased from no herbivory to moderate grazing intensity, and then declined as grazing intensity continued to increase. Compensatory responses by plants likely are more difficult to detect when responses to herbivory are subtle and occur at relatively low grazing intensity. I observed

strong effects of density dependence on physical condition of elk and reductions in NAPP of plant communities with high levels of grazing intensity. At high-population densities resources for elk declined and NAPP was reduced. At low-population density elk were in good physical condition with high rates of reproduction, and NAPP increased, indicating compensatory responses by plants. Density-dependent feedbacks in populations of large herbivores help regulate population dynamics, and those same processes have substantial effects on ecosystem functioning.

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ACKNOWLEDGMENTS

This dissertation includes 4 chapters, each of which is a complete manuscript that has either been published in a peer-reviewed journal, submitted to a peer-reviewed journal, or is destined for submission. Full citations for each manuscript are provided in a footnote on the first page of each chapter. Each citation includes co-authors who contributed significantly to the research for the manuscripts on which they appear. I am senior author on all chapters and I analyzed and collected all of the original data presented in these chapters. I wrote this dissertation and, although my co-authors and committee members have influenced them, the ideas contained herein are mine.

Funding and support for this research was obtained from several sources: the Pacific Northwest Research Station of the US Forest Service, the Institute of Arctic Biology and the Department of Biology and Wildlife at the University of Alaska Fairbanks, the Rob and Bessie Welder Wildlife Foundation, and the Rocky Mountain Elk Foundation. The Graduate School at University of Alaska Fairbanks provided a graduate fellowship and a thesis completion fellowship.

This project would not have been possible without the assistance of many people. First, I would like to thank John Kie and Terry Bowyer, co-chairs of my committee, were incredibly supportive of me throughout this project. I truly enjoy discussing ideas and interpretation of results of analyses with both Terry and John. John extended his hospitality and friendship, and was always available for help when problems arose, as they inevitably do, with study design, field collection and interpretation of data.

Terry Bowyer and his wife, Karolyn, extended their hospitality to me on numerous occasions and for extended periods, including my initial arrival into Fairbanks and on several occasions when I returned from the field to work at the University. Terry's enthusiasm for science is contagious and his extensive knowledge of population ecology, behavior and natural history of numerous species is often staggering and always provides stimulating discussion. Terry and Karolyn also extended their friendship, which I truly appreciate and will continue to treasure.

I also would like to thank my committee members, Roger Ruess and Jim Sedinger, who have both been very supportive throughout this process. They were both extremely helpful in discussing ideas and solving sampling-design problems. I also appreciate their contributions to these manuscripts; their input substantially improved each of the chapters.

I greatly appreciate all of the help I received from Brian Dick, Area Manager of the Starkey Project. Brian was instrumental in helping with data collection, locating sites for exclosures, building 24 exclosures, and clipping vegetation for 3 years. I appreciate all of his efforts in handling elk and deer, for fitting radio collars, and collecting data on reproduction and body condition, and of course for getting the correct number of animals into each study area each year. I enjoyed the time that he spent in the field with me, helping me get to know the habitats and plant communities. I really appreciate everything that he taught to me, including driving tractors, and of course all of the times that he fixed my truck. Brian and his family (Jana and Lindsey) are truly wonderful friends.

Numerous employees from Starkey helped with building exclosures and clipping plants. I truly appreciate the help I received from Ryan Kennedy and Jack Nothwang for clipping plants, in either very hot weather or blowing snow, building and repairing fences for exclosures, and handling of animals, including collecting data and placing radio collars on both mule deer and elk. Numerous volunteers helped with collecting vegetation during summers. Paul Kennington, Leslie Naylor, Amanda Stokes, and Jeremy Anderson, aided in building exclosures and endured several years of clipping plants, I truly appreciate their help. Paul Kennington got up in the middle of the night during winter and recaptured >200 elk that had escaped from the winter feedground, if not for his efforts, we would not have had enough animals to begin the experiment. Rosemary Stussy helped me learn to use ArcView GIS and spent many hours with me in front of the computer, locating possible sites for exclosures. She rapidly became a very close friend.

Finally, I want to thank my family for all of their support throughout my graduate school experience, especially my mom (Louise), dad (Court) and stepdad (Doug). I want to express my love and appreciation to my husband, Thad. Although he married me halfway through this experience, he has been incredibly supportive and encouraging throughout the process. I appreciate his help with data collection in the field and putting collars on both mule deer and elk. I truly enjoy discussing ideas with him, and I appreciate all of the time he has spent listening to me practice talks.

INTRODUCTION

Density dependence plays a key role in life-history characteristics and population ecology of large, herbivorous mammals. Those life-history characteristics, including strong competitive ability, large body size, long lifespan, low reproductive rate and high maternal investment (Clutton-Brock 1987; Gaillard et al. 2000; Kie et al. 2003; McCullough 1979), are influenced by density-dependent processes and likely make them among the most competitive of all organisms (McCullough 1979, 1999; Stearns 1992). Density dependence has been difficult to document because most studies attempting to examine these processes make comparisons across too narrow a breadth of densities with respect to ecological carrying capacity (K) or too short a time span to detect changes in fecundity, recruitment, or survival, and as a result often fail to detect those processes (Kie et al. 2003; McCullough 1990). Because most aspects of the ecology of large mammals are influenced by density-dependent processes, understanding density dependence likely is the key to understanding resource partitioning and competitive interactions among species of large, herbivorous mammals. Moreover a growing body of literature indicates that browsing and grazing by large herbivores can have far-reaching effects on the structure and function of ecosystems (Bowyer et al. 1997; Kie et al. 2003; McNaughton 1985; Turner et al. 1997).

Resource partitioning among species traditionally has been evaluated along 3 niche axes: spatial separation (including use of different habitats), temporal avoidance, and dietary differences (Keddy 1989; Ben-David et al. 1996; Kronfeld-Schor et al. 2001). Experiments investigating resource partitioning and competition among large mammals

have been problematic because conducting addition or removal experiments over sufficiently large areas to study competition or resource partitioning have not been feasible. Moreover exploring niche separation among large herbivores often is formidable because those mammals occupy relatively large home ranges and exhibit broad dietary niches.

An experimental approach to the study of density dependence also has been difficult and few studies have tested effects of high- and low-population density simultaneously in the same ecosystem, again because of the difficulty of performing manipulative experiments on large mammals. Indeed, research substantiating the importance of density-dependent mechanisms in ungulate population typically have come from long-term studies in which populations varied markedly with respect to K and appropriate vital rates for populations were collected (Clutton-Brock et al. 1987; Gaillard et al. 2000; McCullough 1979). Such a design, however, cannot sort stochastic events that occur among years from influences of population density (White and Bartmann 1997). Moreover, comparing densities among populations to evaluate parameters such as recruitment or survival is meaningless without knowledge of where those populations are with respect to K (Bowyer et al. 1999; Kie et al. 2003; McCullough 1979).

The first two chapters of my dissertation investigate resource partitioning among rocky mountain elk (*Cervus elaphus nelsoni*), rocky mountain mule deer (*Odocoileus hemionus hemionus*), and range cattle (*Bos taurus*), because those 3 species frequently co-occur on rangelands in the northwestern United States. In chapter one I examined temporal and spatial relationships among those 3 large herbivores to better understand

how niche partitioning of habitats was affected by differing use of space and whether such differences were maintained over time. Specifically, I hypothesized that niche overlap would be greatest between introduced cattle with the 2 native herbivores (elk and mule deer) because coevolution between elk and mule deer should have resulted in strong patterns of resource partitioning. Finally, because cattle were added to our study area in spring and removed in autumn, we tested for competitive displacement of the native herbivores by cattle during those two seasons and hypothesized that if competition occurred, niche relations between 2 species would differ when a 3rd was added or removed.

In chapter 2, I explored niche separation in diets of mule deer, elk, and cattle and the potential use of stable isotope analyses to examine dietary differences among large herbivores. I hypothesized that these 3 herbivores would exhibit low overlap in use of forages in summer (when the greatest spatial overlap among species occurred; Stewart et al. 2002). Further, I hypothesized that the smaller-bodied species, mule deer, would be more selective in their diets as indicated by less variability among individual diets and by use of higher-quality forages. Finally, I hypothesized that dietary differences among these 3 species would be reflected in their $\delta^{13}C$ and $\delta^{15}N$ signatures.

In chapter 3, I designed a manipulative experiment to examine effects of density-dependent processes in North American elk at high- (near *K*) and low-population (below maximum sustained yield, MSY) densities, simultaneously in the same system. I hypothesized that differences in body condition and reproduction between high and low densities of elk would result from density-dependent processes. If those

density-dependent effects were manifested principally through intraspecific competition, I predicted that body condition and pregnancy rates of adult females would be lower in the high-density population than for the population at low density. Although such data would need to be collected across a wide range of densities and include information on survivorship of young to fit a recruitment curve (sensu McCullough 1979), this experimental manipulation of elk density provides a critical test of whether density dependence in reproduction occurs for this large mammal.

Finally in chapter 4, I investigated effects of density dependence in elk on the habitats and plant communities that they inhabit. This examination of effects of high- and low-density populations of elk on plant communities was conducted simultaneously with that investigation of the effects of density dependence in elk populations. I designed this experiment to investigate the interaction between density dependence and ecosystem processes at high and low population densities of elk. Accordingly, I tested hypotheses relating to herbivore optimization, and how plant productivity was affected by population densities of elk. Herbivore optimization is described as the enhancement of net primary production of forage plants with moderate levels of herbivory above that of ungrazed or heavily grazed plants (Hik and Jefferies 1990). I hypothesized that herbivore optimization would occur as population density of elk increased and there would be a concordant increase in plant production initially followed by a decline in productivity as grazing intensity continued to increase. Following Hik and Jefferies (1990), I hypothesized that changes in NAPP would be most prevalent during the growing season in spring. I also hypothesized that rates of vegetation offtake by elk would increase

concurrent with increasing productivity, and then decline as grazing intensity continued to increase and NAPP declined.

CHAPTER 1[1]

TEMPOROSPATIAL DISTRIBUTIONS OF ELK, MULE DEER, AND CATTLE: RESOURCE PARTITIONING AND COMPETITIVE DISPLACEMENT

Rocky Mountain elk (*Cervus elaphus nelsoni*), Rocky Mountain mule deer (*Odocoileus hemionus hemionus*), and cattle frequently co-occur on landscapes in the northwestern United States. We hypothesized that niche overlap would be greatest between introduced cattle with either of the 2 native herbivores because co-evolution between native elk and mule deer should have resulted in strong patterns of resource partitioning. We observed strong differences among species in use of space, especially elevation, steepness of slope, and use of logged forests. We used 2 temporal windows to examine both immediate (6 h) and long term (7 days) effects of competition. We noted strong avoidance over a 6-h period among 3 ungulates. That effect was weaker for the previous 7 days. Cattle were generalists with respect to habitat selection; the 2 native herbivores avoided areas used by cattle. Mule deer and elk avoided one another during the short temporal window (6 h), although spatial differences in habitat use often were not maintained over 7 days. Elk used lower elevations when cattle were absent and moved to higher elevations when cattle were present, indicating shifts in niche breadth and competitive displacement of elk by cattle. We demonstrated strong partitioning of resources among these 3 species, and presented evidence that competition likely resulted in spatial displacement.

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[1] Stewart, K. M., R. T. Bowyer, J. G. Kie, N. J. Cimon, and B. K. Johnson. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83:229-244.

Key Words: *Cervus elaphus*, competition, competitive exclusion, elk, free-ranging cattle, mule deer, niche partitioning, *Odocoileus hemionus*, Oregon

Understanding how habitat selection affects distributions of large mammals across the landscape is a necessary prerequisite to examining patterns of resource partitioning and competition (Cooke 1997). Competition is difficult to assess without experimentation, because niche partitioning among coexisting species may have resulted from past competitive interactions (e.g., the ghost of competition past; Connell 1980). Despite numerous studies, causes and consequences of competition among large herbivores remain uncertain. This paucity of information on competition among large mammals is unfortunate because their life-history strategies should make them among the most competitive of all organisms (McCullough 1979, 1999; Stearns 1992). Moreover, a growing body of literature suggests that browsing and grazing by large herbivores can have far-reaching effects on the structure and function of ecosystems (Bowyer et al. 1997; McNaughton 1985; Turner et al. 1997 for reviews).

An experimental approach to the study of competition among large, herbivorous mammals has been problematic, because conducting addition or removal experiments concerning competition among ungulates have not been feasible. Indeed, reviews by Keddy (1989) and Schoener (1983) included few examples of competition among large mammals. Thus, most studies of large herbivores infer the effects of competition from the amount of resource or niche partitioning (Jenkins and Wright 1988; McCullough 1980; Putnam 1996; Sinclair 1985). Interactions between native herbivores and domestic

cattle are among the few studies where interference or exploitive mechanisms among large herbivores have been proposed (Hobbs et al. 1996; Jenks et al. 1996; Julander 1958; Kie et al. 1991; Mackie 1970). Indeed, Bowyer and Bleich (1984) and Loft et al. (1987) reported that cattle reduced vegetative cover essential for fawning habitat for mule deer (*Odocoileus hemionus*). Johnson et al. (2000) demonstrated that elk (*Cervus elaphus*) affected the distribution of mule deer during spring but not vice versa. Likewise, Coe et al. (2001) reported stronger competitive interactions between cattle and elk than for mule deer and cattle in summer. Nonetheless, important theoretical and applied questions regarding competition remain unresolved.

We tested hypotheses concerning resource partitioning, habitat selection, and competition among free-ranging cattle, Rocky Mountain elk (*C. e. nelsoni*), and Rocky Mountain mule deer (*O. h. hemionus*). We predicted that resource partitioning would be most pronounced and competition minimized between the 2 native cervids, because past competitive interactions should have resulted in strong patterns of habitat separation. We expected the reverse pattern for relationships of nonnative cattle with mule deer or elk. We also predicted that the 2 species with high dietary overlap that consumed mostly graminoids (elk and cattle—Stevens 1966) would exhibit greater competitive interactions than either cattle or elk with the species that concentrated on forbs (mule deer—Bowyer 1984). We examined the temporospatial relationships among the 3 large herbivores to better understand how niche partitioning of habitats was affected by differing use of space and whether such differences were maintained over time. Finally, because cattle were added to our study area in spring and removed in autumn, we tested for competitive

displacement of the native herbivores by cattle during those seasons. We further hypothesized that if competition occurred, niche relations between 2 species would differ when a 3rd was added or removed.

MATERIALS AND METHODS

Study area.—We conducted research from 1993 through 1995 on the Starkey Experimental Forest and Range (hereafter, Starkey) of the United States Forest Service. Starkey (45° 12' N, 118° 3' W) is situated in the Blue Mountains of northeastern Oregon and southeastern Washington, USA, and is located 35 km southwest of La Grande, Oregon. The area encompasses 10,125 ha, and is surrounded by a 2.4-m high fence that prevents immigration or emigration of large herbivores (Rowland et al. 1997). Elevations range from 1,120 to 1,500 m. This site supports a mosaic of forests and grasslands, with moderately sloping uplands dissected by drainages, which are typical of summer ranges for elk and mule deer in the Blue Mountains (Rowland et al. 1997). Seasons were delineated with a climograph and were defined by months that grouped within similar ranges of temperature and precipitation (Figure 1.1), and reflected changes in plant phenology.

We restricted collection of data and our analyses to the northeast experimental area on Starkey, which was separated from the remainder of Starkey by a fence (Rowland et al. 1997). This northeast area contained 1,453 ha and consisted of 4 major habitats including: (1) mesic forest dominated by grand fir (*Abies grandis*; 25% of the study area); (2) xeric forest characterized by Ponderosa pine (*Pinus ponderosa*; 6% of the study area); (3) xeric grassland dominated by a few grasses and forbs, such as onespike oatgrass

(*Danthonia unispicata*), Idaho fescue (*Festuca idahoensis*) and low gumweed (*Grindelia nana*; 25% of the study area); and (4) logged forest, harvested during 1991-1992 and then seeded with rhizomatous grasses such as orchardgrass (*Dactylis glomerata*) and bluegrasses (*Poa* sp.; 34% of the study area—Rowland et al. 1998). The logged forest was defined as a separate habitat because the composition of plant species, canopy cover, and responses of ungulates differed from the initial forest type. Grand fir in the northeast area suffered widespread mortality (>90%) from spruce budworm (*Choristoneura occidentalis*) and timber was harvested in 1991-1992, predominately in areas where most trees had been killed (Rowland et al. 1997).

Our analyses included periods when all 3 species of ungulates were present on the study area, which typically was from mid-June through mid-October and included spring (only June), summer, and autumn (Figure 1.1). Cattle were present on Starkey from mid-June until mid-October each year; most elk were fed a maintenance diet in a separate facility during winter (Rowland et al. 1997). Hence, only mule deer were present on the study area year-round. All 3 species occurred at moderate population densities relative to carrying capacity (Rowland et al. 1997). Population sizes in the northeast area were approximately 50 adult female cattle (with young), 75 mule deer, and 130 elk as determined from stocking rate and helicopter census (Rowland et al. 1997). We collected data on locations of 118 individual females equipped with radiocollars, including 14 cattle, 18 mule deer, and 25 elk. Cattle were stocked at a moderate to high population density for the Blue Mountains of Oregon (Rowland et al. 1997). Annual recruitment of young elk on Starkey was 35-50 young:100 adult females and averaged 41

(± 9.6 SD) from 1989 to 1995. Recruitment rate on our study area indicated that the population was increasing; however, that increase was well below the maximum finite rate of growth ($\lambda = 1.46$) reported for elk (Kimball and Wolfe 1974). Thus, some resources may have been in short supply, and competition among large herbivores was likely.

Definitions.—We defined exploitive and interference competition in accordance with Park (1962), Birch (1957), Case and Gilpin (1974), and Keddy (1989). Exploitative competition occurs when 1 species uses a limited resource at a rate that reduces its availability to coexisting species. Interference competition results when an individual of a dominant species causes direct harm to another individual via physical, chemical, or behavioral mechanisms; this may occur when one individual directly attacks another or in subtler forms, such as threat behavior or territoriality. Thus, interference competition precludes the use of a resource by a competing species, but does not necessarily remove that resource from the environment.

Both mathematical (Lotka 1932) and empirical (Brown et al. 1979) approaches to understanding competition recognize 2 important components to this process: number of competitors, and their ability to compete (i.e., their competition coefficients). We focus on this second component of competitive interactions among large herbivores, including niche overlap, and aspects of past competition (Connell 1980) or avoidance along particular niche axes.

Geographic information system (GIS) analyses.—Locations of mule deer, elk, and cattle were collected with a rebroadcast LORAN-C system from 1993 to 1995. This

automated telemetry system located each radio-collared animal approximately every 1.5 h over 24 h from June to early November each year (Rowland et al. 1997). Data on animal locations and habitat variables were determined on a 30-m^2 pixel basis from a raster-based GIS maintained by the Oregon Department of Fish and Wildlife and the United States Forest Service (Rowland et al. 1998). A spatial window of 25-pixels (5 pixels by 5 pixels; 2.25 ha) was centered on each animal location to account, in part, for error associated with telemetry locations of animals (Findholt et al. 1996; Johnson et al. 1998).

The telemetry system exhibited differences in location rates of animals that varied spatially across the study area (Johnson et al. 1998). Thus, statistical analyses were weighted by the inverse of the correction factor developed for Starkey in each year to mitigate the effects of telemetry error on our analyses.

Habitat values for percentage of each plant community and means for elevation (m), slope (%), aspect (°), distance to permanent and intermittent water (m), distance to the ungulate-proof fence (m), and distances to roads (m) were calculated to characterize each 25-pixel window, and thereafter used as a single value for that spatial window.

Availability of water varied among seasons, and permanent sources of water consisted primarily of developed springs. Intermittent sources of water, which included a riparian area, typically retained water until mid-summer (July or August), depending on rainfall in June and early July.

We controlled for effects of the ungulate-proof fence by including distance to the fence (m) in stepwise logistic analyses. Potential effects of roads on animals were

evaluated on the basis of different levels of traffic. One road, open to the general public (hereafter, open road), was located outside the ungulate-proof fence on the southwestern border of the study area. Restricted roads were distributed throughout the study area and received moderate use by Forest Service and other research personnel. Closed roads had no traffic. We also calculated an index of diversity of terrain for each spatial window by multiplying the standard deviation of the slope by the mean angular deviation of aspect (Nicholson et al. 1997).

We created a database using 1 randomly chosen location per day for each elk, deer, and cow (June-October, 1993-1995) to help minimize the lack of independence of sample locations. For each animal, we determined the habitat values for its spatial window. We also recorded the total number of telemetered mule deer, elk, and cattle within each window 3 h before and after (6 h total) and during the previous 7 days from the time of the animal location. We chose 6-h and 7-day windows to examine immediate (6 h) and accumulated (7 days) effects of potential competitors over time. Six hours was required to obtain an adequate sample size without encompassing >1 activity period. Seven days was the longest period that allowed for a sufficient number of samples during spring (June) and autumn (October) once data were time lagged for those seasons. We then sampled all telemetered animals without replacement for that day and excluded any animals located within a previously sampled window for that day to maintain independence of animal locations. We repeated that procedure until all animals of each species with radiocollars were located for that day.

After we determined the number of animal locations sampled, we then cast an equal number of random points to calculate availability of habitats and physical characteristics for each spatial window centered on each random point (i.e., 1 random point for each animal location). Using this methodology, we recorded a total of 10,386 animal locations, based upon 57 telemetered animals and 10,386 random points. Locations for radio-collared animals had varying sample sizes depending on the number of years that an animal was present on the study area. To prevent a single animal from having a disproportionate effect on analyses, we subset our data to 1 location animal^{-1} month^{-1} year^{-1} with a total of 465 animal locations and 465 random locations, randomly drawn from our data set of 57 individuals. To assure the aptness of this method, we selected 10 subsets of those data at random for all collared animals and tested means with MANOVA for all habitat variables between subsets of those data. Means of habitat variables were not significantly different ($P > 0.15$) between our data subsets, and we randomly selected one subset for further analyses.

Statistical design.—We used a hierarchical approach for understanding habitat selection and potential competition among cattle, elk, and mule deer (Table 1.1). First, multi-response permutation procedures (MRPP; Slauson et al. 1991) were used to test for differences in spatial distributions among cattle, elk, and mule deer, as well as from random locations (the null model). MRPP offers a powerful method to assess the distributions of mammals (Nicholson et al. 1997; Pierce et al. 2000).

We used logistic regression to identify habitat variables selected (or avoided) by each species (Bowyer et al. 1998, 1999). We employed multivariate analysis of variance

(MANOVA) to test for differences in relative use and availability (selection or avoidance) of habitat variables among species (Bowyer et al. 1998, 1999; Nicholson et al. 1997). We then evaluated the relative importance of the 4 plant communities for each ungulate species (Bowyer and Bleich 1984; Weixelman et al. 1998).

We developed multiple-regression models to test for any remaining competition between those large herbivores with effects of resource partitioning held constant (Fox and Luo 1996; Luo et al. 1998). We incorporated a temporal window of 7 days into multiple-regression models and compared them with the near-instantaneous (6 h) multiple-regression models to evaluate the relative effects of accumulated time on potential competitive interactions. A regression approach may be used to determine competition coefficients under field conditions for sympatric species (Crowell and Pimm 1976; Hallett and Pimm 1979; Schoener 1974). Moreover, the regression method controls for effects of past competitive interactions on existing partitioning of niches (Hallett and Pimm 1979). That method, however, was problematic because estimated coefficients were qualitatively inconsistent and contained statistical artifacts in the relation between competitive ability and census variance (Rosenzweig et al. 1985). Application of a standardization procedure eliminates effects of census variance on coefficients of competition (Fox and Luo 1996; Luo et al. 1998). Thus, the multiple-regression approach allows evaluation of competitive interactions, while controlling for niche partitioning among species.

Statistical analyses.—Before addressing competition among species, we used MRPP to test the null model that species were randomly distributed across the landscape

and that species distributions were random compared with one another. MRPP are distribution-free statistics that rely on permutations of data based on randomization theory and allow analyses of spatial differences not possible with logistic regression, such as partitioning of space within a habitat type (Slauson et al. 1991; Zimmerman et al. 1985). Significant differences from the distribution of random locations by a particular species indicate some type of habitat selection, and significant differences among the distributions of species indicates that there is spatial separation.

We used step-wise logistic regression ($\alpha = 0.15$ to enter and remain) to evaluate variables associated with animal locations (coded 1) and to determine habitat variables that differed significantly from random locations (coded 0) for each species (SAS institute Inc. 1987). We controlled for multicollinearity (Bowyer et al. 1998, 1999) by eliminating 1 of any pair of variables with $r^2 > 0.45$. Distance to the open road was negatively correlated with elevation ($r = -0.70$, $P < 0.001$). Because the open road was outside the study area, that variable was eliminated from our analyses to avoid problems with multicollinearity. We evaluated the aptness of logistic models with a Hosmer-Lemeshow test for goodness-of-fit (Agresti 1990). Because animals may have been present at a random location other than when we sampled, our analysis provided a conservative measure of habitat selection (Bowyer et al. 1998). A logistic model was fit for all species (including species as a coded variable) and then separate models were analyzed for each species to reduce dimensionality of data. This approach has been used previously to examine habitat selection within and among species of mammals (Bowyer et al. 1998, 1999).

Habitat variables selected from logistic regression were used to develop a MANOVA model to evaluate differences in habitat selection among species. We performed an arcsine-squareroot transformation on percentage data and a squareroot transformation on the number of animals within each spatial window to satisfy distributional assumptions of MANOVA (Johnson and Wichern 1992). We transformed aspect (a circular variable) to Cartesian coordinates (sine and cosine) prior to analyses (Zar 1996).

We used MANOVA to determine interspecific differences in habitat selection within seasons, and to test for significant species (cattle, elk, or mule deer) by location (animal or random) interactions (i.e., differences in selection among species). Habitat characteristics were dependent variables and main effects were animal location (use vs. random), species (cattle, elk, mule deer) and season (spring, summer, autumn). Significant location-by-species interactions indicated differences in selection (use > availability) or avoidance (use < availability) among species (Bowyer et al. 1998, 1999; Nicholson et al. 1997; Rachlow and Bowyer 1998; Weixelman et al. 1998). We then used ANOVA with planned contrasts to separate significant differences ($P \leq 0.05$) in means of habitat variables between species.

For descriptive purposes only, mean values for each habitat variable for random locations (available) were subtracted from mean values of animal locations (used) and divided by the sum of those values to allow for comparisons without extreme differences in units measured; a positive result typically indicated selection and a negative one indicated avoidance (Powell et al. 1997). Bivariate plots of 95% *CI* for variables that

differed among species were plotted to further elucidate resource partitioning among species. We also determined the relative importance of each habitat type seasonally. Importance was defined as use times availability rescaled to 100% (Bowyer and Bleich 1984; Weixelman et al. 1998). This approach allows evaluation of habitat components that are crucial to a species, but are not limited in supply. Logistic regression will not identify such habitats (Bowyer et al. 1999).

We determined interspecific associations using multiple-regression analyses for each species with habitat variables that differed in selection among species included as covariates (Fox and Luo 1996; Luo et al. 1998). We used Mallow's *Cp* to aid in model selection; this statistic provides information similar to that from Akaike's information criterion (Atilgan 1996). Variables representing number of animals within each spatial window (for either 6 h or 7 days) were standardized prior to analyses to prevent biases associated with the correlation between regression coefficients and variances of the independent variables (Fox and Luo 1996; Luo et al. 1998; Marquandt 1980). We used separate regression models to evaluate temporal effects (e.g., 6 h and 7 days) for each species. Model fit was evaluated with the adjusted coefficient of multiple determination (R^2_a), to account for the number of independent variables in the multiple-regression model (Zar 1996). The dependent variable for both regression models (6 h and 7 days) consisted of 1 of the 3 species within 6 h of a particular animal location. For example, number of elk within 6 h of an animal location was the dependent variable in regression models to evaluate effects of cattle and mule deer on elk. Independent variables for 6-h models included the number of the 2 sympatric species within 6 h ($\pm$ 3 h) of the time of

location, and habitat variables from MANOVA that differed in selection among species. For 7-day models, independent variables included the accumulated number of all species within the previous 7 days, and habitat variables from MANOVA that differed in selection among species. Those habitat variables that were included in the regression model behaved as covariates in multiple-regression analyses (Zar 1996). Standardized regression coefficients of independent variables for sympatric species, located within each spatial window (6 h or 7 days), were estimated coefficients of association (α_{ij}) and indicated the effect of the 2 sympatric species on the third species (e.g., dependent variable). Fox and Luo (1996) provide a more complete description of this method. Because our data for animal counts within the spatial windows were standardized prior to analyses, the estimated coefficients of association ranged between 1 and −1. A coefficient of 1 indicates complete spatial overlap, a coefficient of −1 indicates spatial avoidance, while a value of 0 or nonsignificance for that variable indicates no effect.

Our interpretations of results from multiple-regression analyses differ slightly from traditional competition coefficients, because those coefficients likely represented differential use of space among species rather than intensity of competition. This different interpretation is required because our dependent variables in multiple regression analyses are strongly representative of where those species already occur across the landscape and are less dependent on the locations of competitors. Strongly negative regression coefficients in our models indicate low spatial overlap among species, rather than 1 species being a more efficient competitor (Fox 1999).

After reviewing results from multiple regressions, we observed that avoidance among species was not maintained over a long time period. Moreover, because we suspected that the 2 native herbivores avoided cattle, we performed an *a posteriori* test of competition between the native herbivores and cattle. We returned to the original data and selected 2 periods, 2 weeks before and 2 weeks after cattle were introduced to the study area during spring and removed in autumn from each year. We again subset data to prevent any single animal from having a disproportionate effect on analyses; thus, this data set contained 492 locations for elk and 244 locations for mule deer. We used the presence of cattle as a treatment effect and compared relative responses of mule deer and elk to the introduction of cattle using MANOVA. The 2 variables in which cattle and the 2 native herbivores partitioned resources were slope and elevation. Thus, the MANOVA model used those variables to compare responses of elk and mule deer to introduction and removal of cattle.

RESULTS

Nearest-neighbor distances of elk (1971 m), mule deer (1487 m), cattle (2011 m), and random (2038 m) indicated some differences in use of space across seasons. Both elk ($P < 0.01$) and mule deer ($P < 0.01$) differed from random locations (e.g., the null model), signifying that selection of habitat occurred (i.e., locations of animals were clumped spatially compared with random samples). Cattle did not differ ($P = 0.10$) spatially from random points. When distributions of species were compared, all 3 species differed ($P < 0.01$) spatially from one another with seasons combined ($P < 0.001$), and

also when seasons were tested separately ($P \leq 0.001$). During spring, however, locations of elk and mule deer did not differ ($P = 0.18$) spatially from each other.

We modeled habitat selection for each species of large herbivore with logistic regression, including plant community, physical characteristics of the landscape, distances to roads, distances to sources of water, and distance to the fence (Table 1.2). None of our models deviated from a logistic fit ($P > 0.26$, Hosmer-Lemshow tests for goodness-of-fit). Year did not enter any logistic model ($P > 0.15$), indicating no yearly differences in habitat selection among species. Likewise, no fence effect on habitat selection by cattle, elk, or mule deer occurred ($P > 0.15$). Distances to water sources and either elevation or slope entered all logistic models, and strongly influenced the distribution of the 3 species (Table 1.3). The logistic model for cattle was 66% concordant and indicated strong affects of slope and distance to sources of permanent water (Table 1.3). Logistic models for elk (67% concordant) and mule deer (73% concordant) indicated selection for several vegetation communities; elk selected both mesic forests and logged forests, and mule deer avoided xeric grasslands (Table 1.3). Elevation and distance to sources of intermittent water also entered logistic models for both elk and mule deer (Table 1.3).

Habitat selection differed among seasons for these 3 large herbivores (*Wilks' Lambda* $P = 0.015$). MANOVA revealed a species (cattle, elk, mule deer) by location (used, random) interaction (*Wilks' Lambda* $P < 0.001$), indicating differences in selection of some habitat variables among species. Univariate analyses following MANOVA identified elevation, slope, and use of logged forest as the only variables in which

selection differed ($P < 0.01$) among species (Figure 1.2). Although there were some differences in selection of xeric grasslands, those differences were marginally not significant ($P = 0.075$, Figure 1.2). Both native herbivores (elk and mule deer) selected higher elevations and steeper slopes than did cattle, especially during spring and summer (Figure 1.2). Bivariate plots of 95% *CI* indicated that cattle differed from the native herbivores by avoiding steeper slopes and high elevations, particularly during spring and summer (Fig. 1.3). Hence, during all seasons elk and mule deer partitioned physical characteristics of the landscape from cattle by occupying higher elevations and steeper slopes (Figures 1.2 and 1.3). Mule deer and elk strongly overlapped in use of slope and elevation, and partitioned use of vegetation communities (Figures 1.2 and 1.3). Elk selected the logged forest and differed ($P < 0.01$) from mule deer and cattle; this differential use of logged forests and possibly of xeric grasslands were particularly evident during autumn (Figures 1.2 and 1.3).

Mesic-forest habitat was of greatest importance to all 3 species (Figure 1.4), although there was no difference in selection of that habitat among species (Figure 1.3). The logged forests and xeric grasslands were of intermediate importance, and the xeric forests were the least important plant communities to these large herbivores (Figure 1.4).

Differences in habitat use by cattle, elk, and mule deer were stronger over the 6-h period than for the previous 7 days (Table 1.4). Coefficients of association for the 6-h models were strongly negative, indicating strong avoidance among all species during all seasons (Table 1.5). The relative effect of resource partitioning on habitat selection was controlled in both 6-h and 7-day models, because habitat variables from MANOVA that

differed in selection among species were included as co-variates in those models. We also included xeric grasslands because they were marginally nonsignificant ($P = 0.075$).

We observed a season by species by treatment interaction (*Wilks' Lambda* $P = 0.046$), as well as a species by treatment interaction (*Wilks' Lambda* $P = 0.002$) for use of slope and elevation by elk and mule deer following introduction and removal of cattle during spring and autumn. We then analyzed species (elk and mule deer) and seasons (spring and autumn) separately. Presence or absence of cattle did not affect use of slopes by elk (Figure 1.5). Mule deer moved to lower elevations following the introduction of cattle during spring. Addition of cattle did not affect use of slope by mule deer during spring, although mule deer moved to more level slopes following removal of cattle during autumn (Figure 1.5). Elk used higher elevations following the addition of cattle during spring and moved to lower elevations following the removal of cattle during autumn (Figure 1.5).

DISCUSSION

We predicted that resource partitioning would be more pronounced between the 2 native herbivores than for either cervid with introduced cattle. Co-existence between deer and elk was expected to result in evolution of strong patterns of habitat or dietary separation. Indeed, we observed strong evidence of resource partitioning of habitats and space among all 3 species of large herbivores (Figures 1.2 and 1.3). Cattle differed from mule deer and elk in avoidance of steep slopes and high elevations. Although the native herbivores selected similar slopes and elevations, mule deer and elk strongly partitioned use of vegetation communities (Figures 1.2 and 1.3). These observations also are

supported by significant differences among species in use of space as indicated by MRPP. Mule deer (Bowyer 1984), elk (Bowyer 1981) and cattle (Kie and Boroski 1996) are constrained in their distribution by availability of free water; all 3 species selected areas nearer to water than at random (Table 1.3). These herbivores did not differ, however, in selection of water resources (Figure 1.2).

Some characteristics of our study site held the potential to affect our results. Distance to the ungulate-proof fence failed to enter any of the logistic models for evaluating habitat selection. That outcome indicated the fence was not a significant factor in affecting habitat selection or distributions of animals on Starkey. Although restricted roads entered logistic models for elk, no differences existed in selection or avoidance of roads among species, suggesting the use of restricted roads did not affect our analyses. Likewise there were no differences among years in selection of habitats by the 3 herbivores.

Coe et al. (2001) noted avoidance of cattle by elk on Starkey. Their results were based on differences between species in "convexity," a variable associated with terrain that measured use of ridgetops and drainage bottoms. That outcome is similar to our findings of resource partitioning based on elevation and slope.

Cattle were habitat generalists when locations were pooled across seasons. Indeed, MRPP did not detect differences between cattle locations and random sites, and no vegetation types entered the logistic-regression models for cattle (Table 1.3). Cattle used more level slopes and lower elevations than did elk or mule deer (Figures 1.2 and 1.3).

Strong, negative coefficients of association in the 6-h regression models indicate spatial avoidance by either 1 or both species (Table 1.4). Indeed, MRPP indicated that all 3 species differed significantly from one another in use of space. Mule deer and elk may have avoided cattle, as indicated by strong negative coefficients in the 6-h models for cattle, and for the cattle variable in the mule deer and elk models. That analysis could not determine if negative coefficients between mule deer and elk in both 6-h models resulted from mutual avoidance or 1 species consistently avoiding the other.

Effects of resource partitioning may be examined when the 6-h and 7-day models are considered together. Strongly negative coefficients for the 6-h period indicate spatial avoidance and any remaining effects that may be attributed to competition are indicated in the 7-day model. Negative coefficients indicate avoidance over the short term, (e.g., 6-h models) and possibly interference or exploitive competition with maintained avoidance over the previous 7 days; those patterns of avoidance may be maintained by interference effects or by the removal of resources by a competitor (e.g., exploitive competition). Conversely, positive coefficients in the 7-day models indicated that the avoidance observed in the 6-h models was not maintained and there was high spatial overlap for the longer period. Hence, those large herbivores used the same habitat, which may be indicative of exploitive competition, particularly during autumn. Large, positive values for coefficients among conspecifics in the 7-day models for mule deer support that observation. Intraspecific competition for female herbivores may be intense (McCullough 1979). When the 7-day models for elk and mule deer are considered together, coefficients of association for mule deer in the 7-day models for elk were

consistently not significant; however, effects of elk on mule deer were significant for all seasons, except spring. Thus, mule deer are more strongly affected by the movements of elk than elk are influenced by mule deer. Moreover, the strong habitat partitioning observed for summer indicated by significant negative coefficients in the mule deer model may be driven by mule deer avoiding elk. During autumn, coefficients of association for elk on mule deer were positive and significant, indicating spatial overlap; changes in forage quality as summer progresses to autumn likely forced mule deer to move into areas used by elk, thereby increasing spatial overlap and likely resulting in exploitive competition. Johnson et al. (2000) noted that mule deer ostensibly avoided elk in spring on Starkey. Although our data did not support their observations during spring, we observed similar patterns of movements by mule deer during summer.

Resource partitioning of dietary niche may result in high overlap in habitat use without increasing competitive interactions (Hanley 1984; Krebs et al. 1974; MacArthur and Pianka 1966). Although we did not measure dietary differences, habitat selection is highly correlated with forage availability in large herbivores (Hanley 1984); thus, high overlap on the habitat axis may be accompanied by low overlap on a dietary niche axis (Kie and Bowyer 1999, Krebs et al. 1974; MacArthur and Pianka 1966). Although overlap in habitat use has been reported to be high for deer and elk, diet overlap is probably relatively low when forage is abundant, because elk are more likely to feed upon graminoids than do mule deer, whereas mule deer feed primarily on forbs and browse (Bowyer 1984; Hanley 1984; McCullough 1980). Seasonal changes in forage availability, however, often lead to increased dietary overlap as forage resources become

less available (Schwartz and Ellis 1981). Indeed, increased dietary overlap has been reported between cattle and elk (Stevens 1966), mule deer and elk (Mower and Smith 1989) and mule deer and cattle (Bowyer and Bleich 1984) in other areas during periods when forage abundance and availability were reduced. We observed high spatial overlap during autumn. Moreover, with the exception of elk, the strongly positive coefficients during autumn when resources are most limiting support that observation; intraspecific effects would be stronger than interspecific ones because of dietary overlap among conspecifics. Thus, we hypothesize that those large herbivores were competing for resources (Table 1.5). Moreover, positive coefficients of association, particularly during autumn, likely indicated exploitive competition.

We hypothesized, *a posteriori*, that the introduction of cattle on to the study area might result in changes in niche breadth among the native herbivores, especially the use of slope and elevation. Indeed, cattle differed from the native herbivores by using lower elevation sites with shallower slopes. Comparisons of elevation and slope prior to and following addition of cattle during spring and prior to and following removal of cattle in autumn indicated that competitive displacement likely occurred between cattle and elk, although we could not control for effects of season in that analysis. Indeed, during spring and autumn, elk used lower elevations when cattle were not on the study area and used higher elevations when cattle were present. We suggest that the corresponding shift in niche breadth of elk indicates competitive displacement by cattle (Hardin 1960; Levin 1970). Mule deer shifted to more level slopes following removal of cattle during autumn. During spring, however, shifts in use of higher to lower elevations following the

introduction of cattle indicated a more complicated response. During spring, mule deer may have responded to elk movements to higher elevations following the addition of cattle to the study area.

Cattle seldom used areas with steep slopes and were widely distributed across vegetation communities at low elevations. These introduced herbivores selected nearness to sources of water, which included riparian zones. Consequently, we hypothesize that sensitive riparian areas at low elevations would require more protection from overgrazing by cattle than those on steep slopes or at high elevations with rugged terrain.

Most studies concerning niche partitioning among large herbivores have not considered cascading effects of competition between 2 species on a 3rd. Thus, studying only 2 of these large herbivores would not have revealed how the niche dynamics of cattle, elk, and mule deer were interconnected. Moreover, in the absence of data on cattle, measuring either habitat use or selection might lead to misinterpreting the habitat requirements of elk and mule deer, and subsequent errors in managing habitat for those ungulates.

We observed substantial resource partitioning in use of slope, elevation, and vegetative communities by cattle, elk, and mule deer. We also demonstrated changes in niche breadth of elk following the addition and removal of cattle from the study site, which likely indicated competitive displacement. Nonetheless, most aspects of the ecology of large mammals are influenced by density-dependent mechanisms (McCullough 1979, 1999) and that observation holds for understanding competitive interactions among large herbivores. Competition is a function of both the number of

competitors and their ability to compete effectively. When there is a large overlap on one or more niche axes, avoidance or partitioning would be expected on another axis (Kie and Bowyer 1999; McCullough 1980). Although we strongly inferred that competition occurred, the ungulates we studied also were strongly partitioning habitats and space. At much higher density, however, the ability to partition space would be reduced, and dietary and habitat partitioning might be intensified. Niche partitioning among populations at high densities becomes more difficult as resources become more limiting, leading to more competition. Such tradeoffs among use of space, diet, and habitats have been documented with increasing population density for the sexes of white-tailed deer (*Odocoileus virginianus;* Kie and Bowyer 1999). A manipulative experiment examining the effects of density-dependent processes on partitioning of space, habitat, and diet holds the most promise for understanding both resource partitioning and competition among large herbivores.

ACKNOWLEDGMENTS

We appreciate the assistance of the Starkey Project personnel including: A. A. Ager, C. Borum, B. L. Dick, S. Findholt, R. Kennedy, J. Nothwang, J. H. Noyes, R. J. Stussy, P. Cole, M. J. Wisdom. D. Thomas and E. Rexstad provided valuable statistical assistance and insight. J. S. Sedinger, R. W. Ruess, D. R. Klein, M. Ben-David, S. Demarais, B. L. Dick, F. Weckerly, R. A. Riggs, B. Person, and K. Hundertmark provided helpful comments on this manuscript. This study was funded by the United States Forest Service and the Institute of Arctic Biology at the University of Alaska Fairbanks.

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Submitted 5 February 2001. Accepted
Associate Editor was T. J. O'Shea.

Table 1.1.—Hypotheses related to niche partitioning by cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) and statistical procedures used to test them; further descriptions and rationale for statistical tests and their citations are provided in materials and methods.

Hypotheses	Statistical tests
Null model	
Animals are distributed randomly across the landscape.	MRPP[a] (used versus random locations for each species)
Species use of space differs across the landscape	MRPP (locations used by each species)
Habitat selection	
Habitat variables are selected, avoided or are important for each species	Stepwise logistic regression by species (used versus random locations)
Species select habitat components differently	MANOVA[b] with main effects location (used, random), species (mule deer, elk, cattle), season (spring, summer, autumn)

Table 1.1.—Continued.

Hypotheses	Statistical tests
Interspecific associations	
Relative influence of interference versus exploitive competition	Multiple regression 6-h and 7-day regression models for each species.
Effects of cattle	
Mule deer and elk are displaced by cattle	MANOVA with main effects species (mule deer, elk) habitat (slope, elevation) season (spring, autumn)

[a] Multi-response permutation procedures.
[b] Multivariate analysis of variance.

Table 1.2.—Summary statistics of habitat characteristics for locations of 3 species of large herbivores (used) and random locations (available) on the Starkey Experimental Forest and Range, northeast Oregon, USA, 1993-1995. Habitat types are expressed as the mean percent of each habitat in a 150 x 150 m spatial window surrounding each animal and random location.

Habitat variables	Cattle (n = 124)		Elk (n = 183)		Mule Deer (n = 158)		Random (n = 465)	
	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*
Mesic forest (%)	0.37	0.03	0.41	0.02	0.41	0.03	0.40	0.01
Xeric forest (%)	0.09	0.02	0.04	0.01	0.11	0.02	0.07	0.01
Logged forest (%)	0.26	0.03	0.33	0.02	0.24	0.03	0.26	0.01
Xeric grasslands (%)	0.27	0.03	0.22	0.02	0.25	0.02	0.29	0.01
Slope (%)	13.3	0.46	15.3	0.39	15.5	0.49	15.3	0.25
Aspect (°)	119.3	8.88	136.6	6.97	140.2	7.26	131.7	4.07
Elevation (m)	1252	5.5	1287	3.9	1299	3.4	1267	2.6
Terrain	118.84	12.52	115.56	8.46	113.77	8.76	131.18	5.90
Distance to permanent water (m)	357.60	19.53	387.86	14.00	326.84	12.88	401.10	9.35

Table 1.2.—Continued.

Habitat variables	Cattle (n = 124)		Elk (n = 183)		Mule Deer (n = 158)		Random (n = 465)	
	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*
Distance to intermittent water (m)	726.37	51.18	803.59	38.22	739.14	39.54	859.55	26.18
Distance to fence (m)	581.79	30.88	596.05	23.80	598.29	27.63	625.88	17.66
Distance to open roads (m)	1170.43	56.05	918.40	37.96	750.99	30.85	1113.35	25.52
Distance to restricted roads (m)	86.53	6.05	92.92	4.62	96.94	5.52	85.02	2.67
Distance to closed roads (m)	546.73	32.72	677.60	25.82	593.75	23.12	602.27	16.31

Table 1.3.—Results of weighted logistic-regression from models of habitat selection for cattle, elk *(Cervus elaphus)*, and mule deer (*Odocoileus hemionus*) on the Starkey Experimental Forest and Range, northeastern Oregon, 1993-1995. Animal locations were coded 1 and random locations were coded 0. Hosmer-Lemshow tests for goodness-of-fit indicated models did not deviate ($P > 0.10$) from logistic fit.

Variable	Parameter Estimate	*SE*	*P*-value
All species			
Intercept	-7.74	2.020	< 0.001
Logged forest	0.44	0.198	0.027
Elevation	0.01	0.002	< 0.001
Slope	- 0.04	0.016	0.001
Distance to restricted roads	< 0.01	0.001	0.016
Distance to permanent water	< - 0.01	< 0.001	0.016
Distance to intermittent water	< - 0.01	< 0.001	< 0.001
Cattle			
Intercept	2.35	0.696	< 0.001
Slope	- 0.12	0.035	< 0.001
Distance to permanent water	< - 0.01	< 0.001	0.037

Table 1.3.—Continued.

Variable	Parameter Estimate	*SE*	*P*-value
Elk			
Intercept	- 9.53	3.255	0.003
Mesic forest	0.64	0.361	0.075
Logged forest	1.16	0.367	0.002
Elevation	0.01	0.002	0.007
Distance to restricted roads	< 0.01	0.002	0.070
Distance to intermittent water	< - 0.01	< 0.001	0.015
Mule Deer			
Intercept	- 21.86	4.781	< 0.001
Xeric grasslands	- 0.78	0.426	0.068
Aspect	- 0.34	0.228	0.140
Elevation	0.02	0.004	< 0.001
Distance to permanent water	< - 0.01	< 0.001	0.022
Distance to intermittent water	< - 0.01	< 0.001	0.027

Table 1.4.—Multiple-regression models, weighted by correction factor for radio telemetry, to evaluate competitive interactions among cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) on the Starkey Experimental Forest and Range in northeastern Oregon, 1993-1995. All models were significant ($P < 0.001$).

	±3 hour model			-7 day model		
Model and Season	*df*	*F*	R^2_a	*df*	*F*	R^2_a
Cattle						
Spring	6, 92	36.07	0.682	7, 91	9.43	0.376
Summer	6,277	113.55	0.705	7,276	6.84	0.126
Autumn	6, 75	24.04	0.631	7, 74	12.26	0.493
Overall	6,458	241.10	0.674	7,457	20.25	0.225
Elk						
Spring	6, 92	41.33	0.712	7, 91	4.07	0.180
Summer	6,277	141.74	0.749	7,276	10.85	0.196
Autumn	6, 75	32.87	0.703	7, 74	12.44	0.497
Overall	6,458	199.62	0.720	7,457	16.93	0.194
Mule deer						
Spring	6, 92	43.47	0.722	7, 91	5.05	0.224
Summer	6,277	131.02	0.733	7,276	7.88	0.145

Table 1.4.—Continued

Model and Season	±3 hour model			-7 day model		
	df	*F*	R^2_a	*df*	*F*	R^2_a
Mule deer						
Autumn	6, 75	27.16	0.660	7, 74	4.83	0.249
Overall	6,458	188.55	0.708	7,457	11.34	0.135

Table 1.5.—Standardized competition coefficients (α) for 3 sympatric ungulates during spring, summer, and autumn as determined from weighted multiple regressions, Starkey Experimental Forest and Range, northeastern Oregon, 1993-1995. Number of conspecifics plus the focal animal in the $\pm$3-h models is the dependent variable for both 3-h and 7-day models.

Competitive Effect	Season			
	Spring (α_{ij})	Summer (α_{ij})	Autumn (α_{ij})	Overall (α_{ij})
Cattle model				
$\pm$3 hour model				
Elk	- 0.790 ***	- 0.866 ***	- 0.831 ***	- 0.828 ***
Mule deer	- 0.773 ***	- 0.823 ***	- 0.714 ***	- 0.785 ***
-7 day model				
Cattle	0.309 ***	0.178 **	0.475 ***	0.275 ***
Elk	0.028 ns	- 0.161 **	- 0.167 *	- 0.106 **
Mule deer	- 0.225 **	- 0.051 ns	- 0.343 ***	- 0.148 ***
Elk model				
$\pm$3 hour model				
Cattle	- 0.714 ***	- 0.736 ***	- 0.669 ***	- 0.716 ***
Mule deer	- 0.818 ***	- 0.803 ***	- 0.738 ***	- 0.790 ***

Table 1.5.—Continued.

Competitive Effect	Season							
	Spring (α_{ij})		Summer (α_{ij})		Autumn (α_{ij})		Overall (α_{ij})	
-7 day model								
Cattle	- 0.071	ns	- 0.137	**	- 0.680	***	- 0.251	***
Elk	0.386	***	0.403	***	0.046	ns	0.327	***
Mule deer	0.079	ns	- 0.071	ns	- 0.011	ns	- 0.049	ns
-7 day model								
Cattle	- 0.071	ns	- 0.137	**	- 0.680	***	- 0.251	***
Elk	0.386	***	0.403	***	0.046	ns	0.327	***
Mule deer	0.079	ns	- 0.071	ns	- 0.011	ns	- 0.049	ns
Mule deer model								
±3 hour model								
Cattle	- 0.676	***	- 0.741	***	- 0.658	***	- 0.707	***
Elk	- 0.789	***	- 0.852	***	- 0.844	***	- 0.823	***
-7 day model								
Cattle	- 0.182	ns	0.071	ns	0.413	***	0.034	ns
Elk	- 0.176	ns	- 0.309	***	0.252	*	- 0.212	***
Mule deer	0.135	ns	0.161	**	0.216	*	0.168	***

*** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P \leq 0.05$, ns = $P > 0.05$.

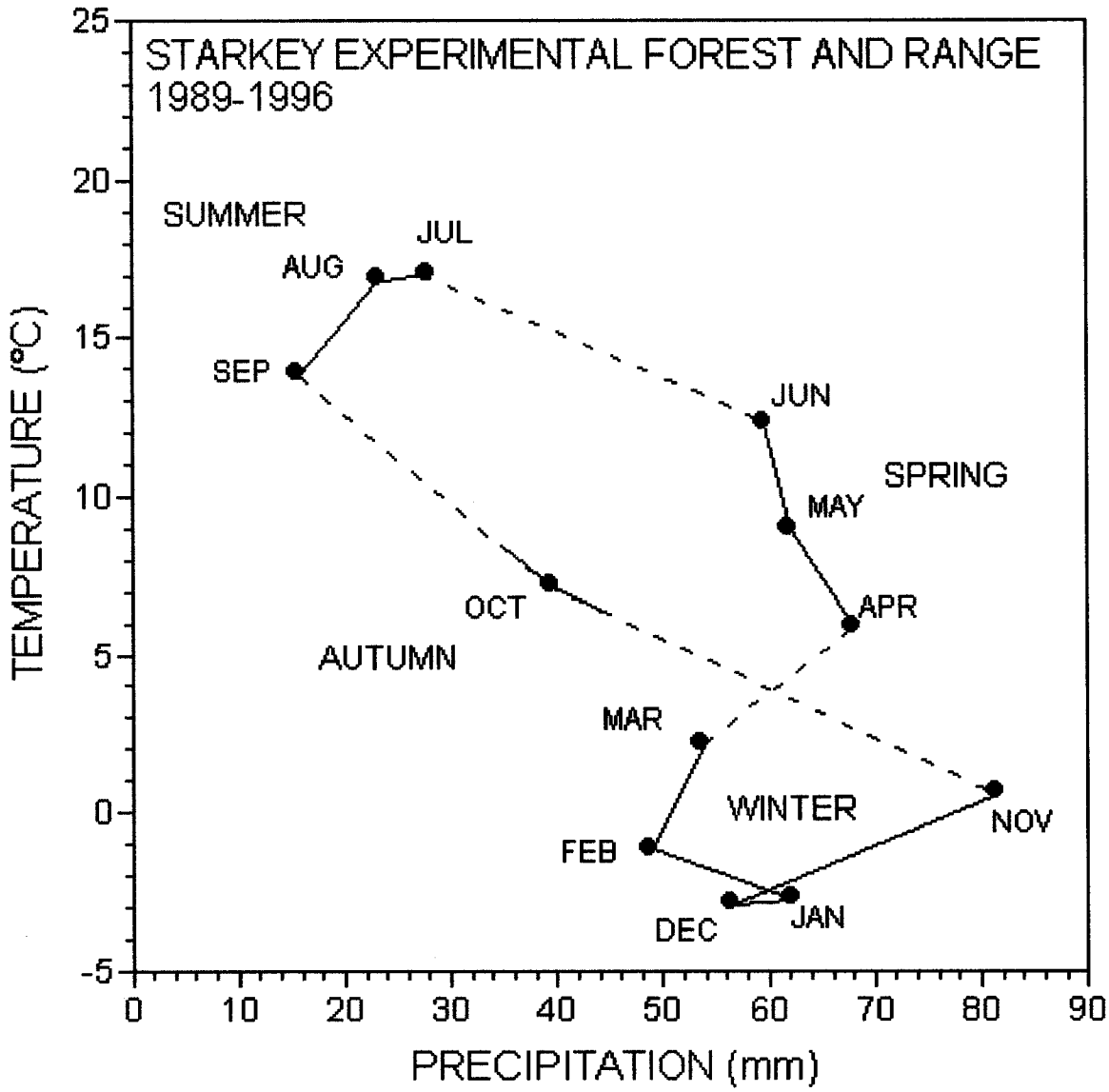

Figure 1.1.—Climograph of mean monthly temperature and precipitation that define seasons on the Starkey Experimental Forest and Range, Oregon, 1989-1996. Solid lines indicate months within a particular season and dotted lines separate seasons.

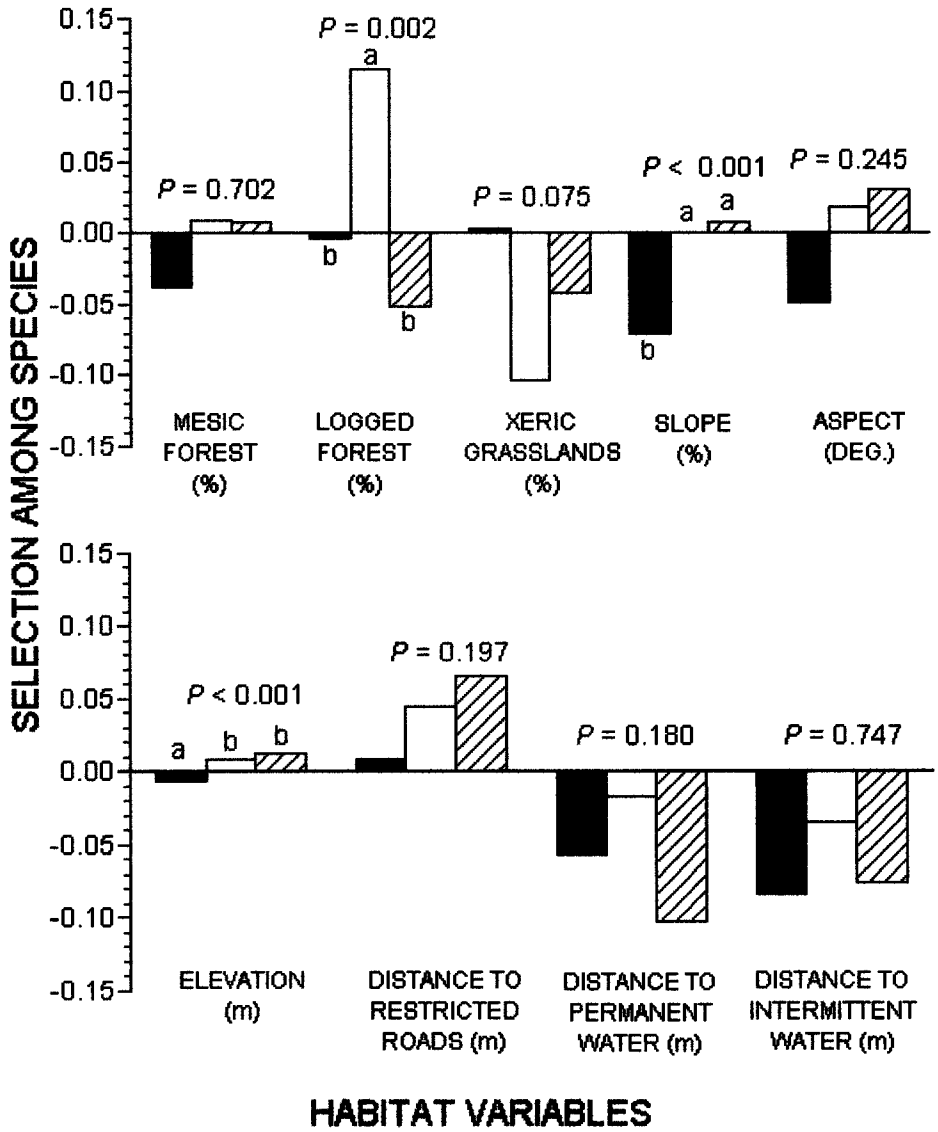

Figure 1.2.—Selection (used minus available, divided by used + available) of habitat variables between cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) on the Starkey Experimental Forest and Range, Oregon, 1993-1995. Values for selection vary from 1 to -1 and negative values for distance measurements indicate selection (i.e., animals are closer than predicted from random). *P*-values are from ANOVA with planned contrasts, following significant differences in selection or avoidance of habitat determined from MANOVA (Wilks' Lambda $P < 0.001$). Differences in lowercase letters indicate significant ($P < 0.05$) differences.

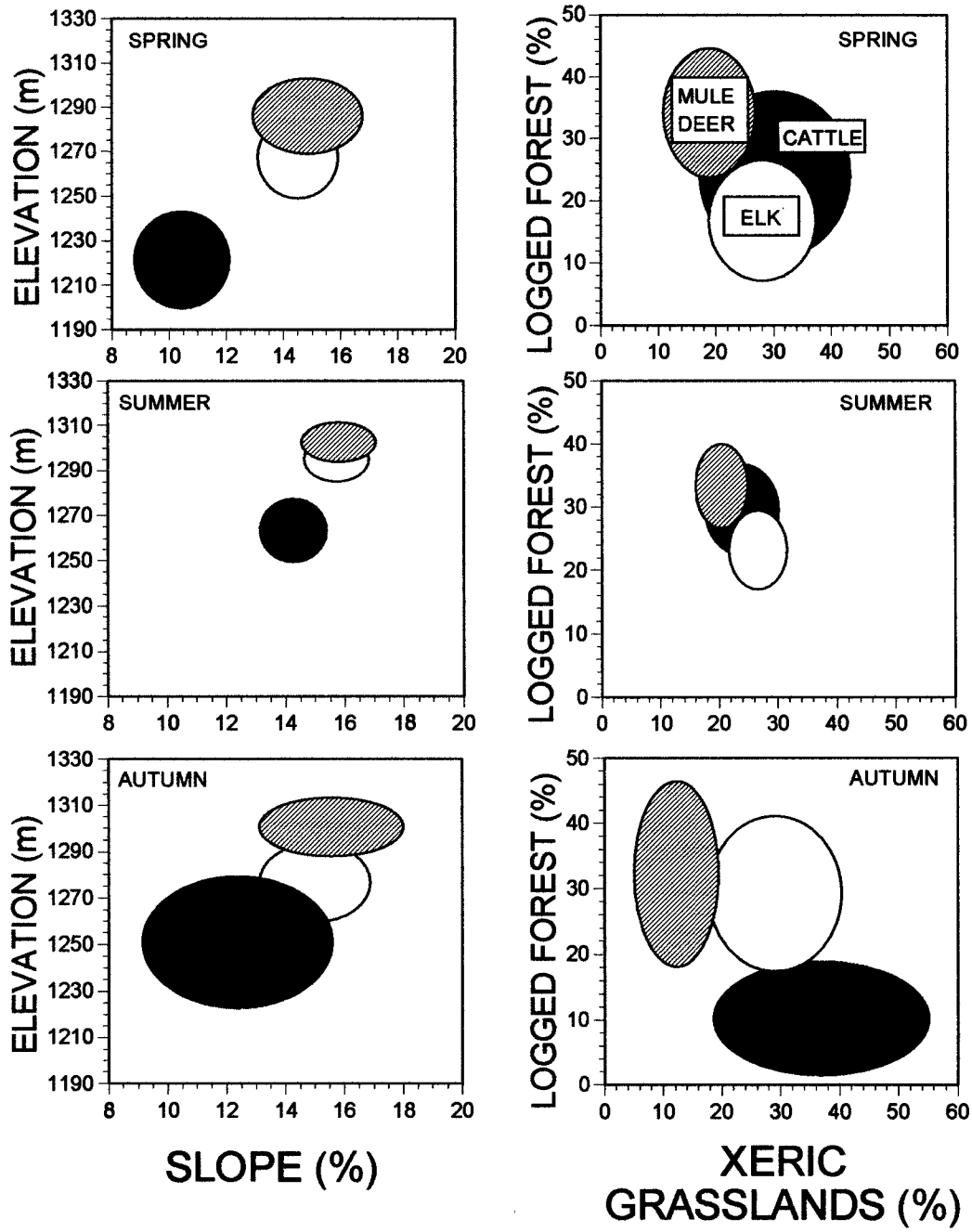

Figure 1.3.—Bivariate plots of niche partitioning based on elevation and slope (left) and logged forest and xeric grasslands (right). Ellipses are 95% *CI* for cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*), across seasons on the Starkey Experimental Forest and Range, Oregon, 1993-1995.

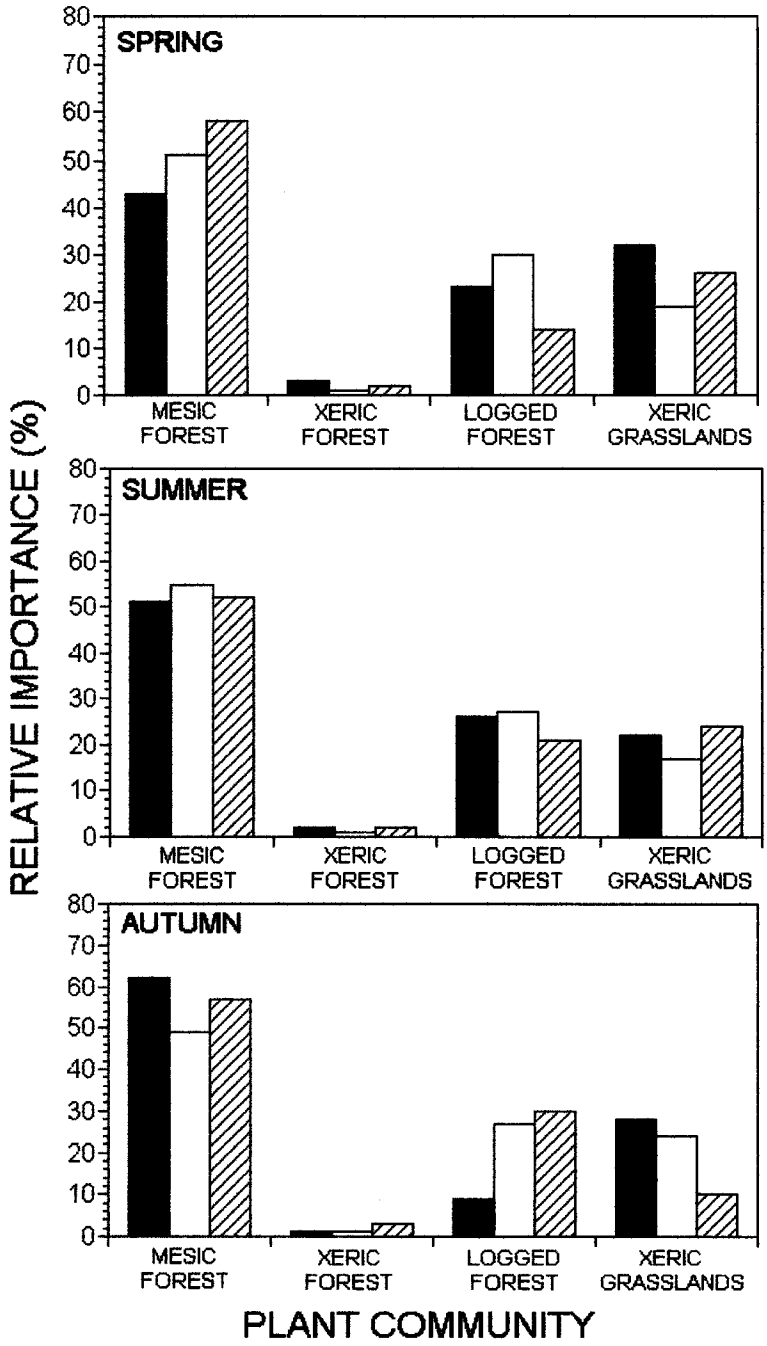

Figure 1.4.—Seasonal importance of vegetation communities for cattle, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) on the Starkey Experimental Forest and Range, Oregon, 1993-1995. Importance is defined as use times availability, rescaled to 100%.

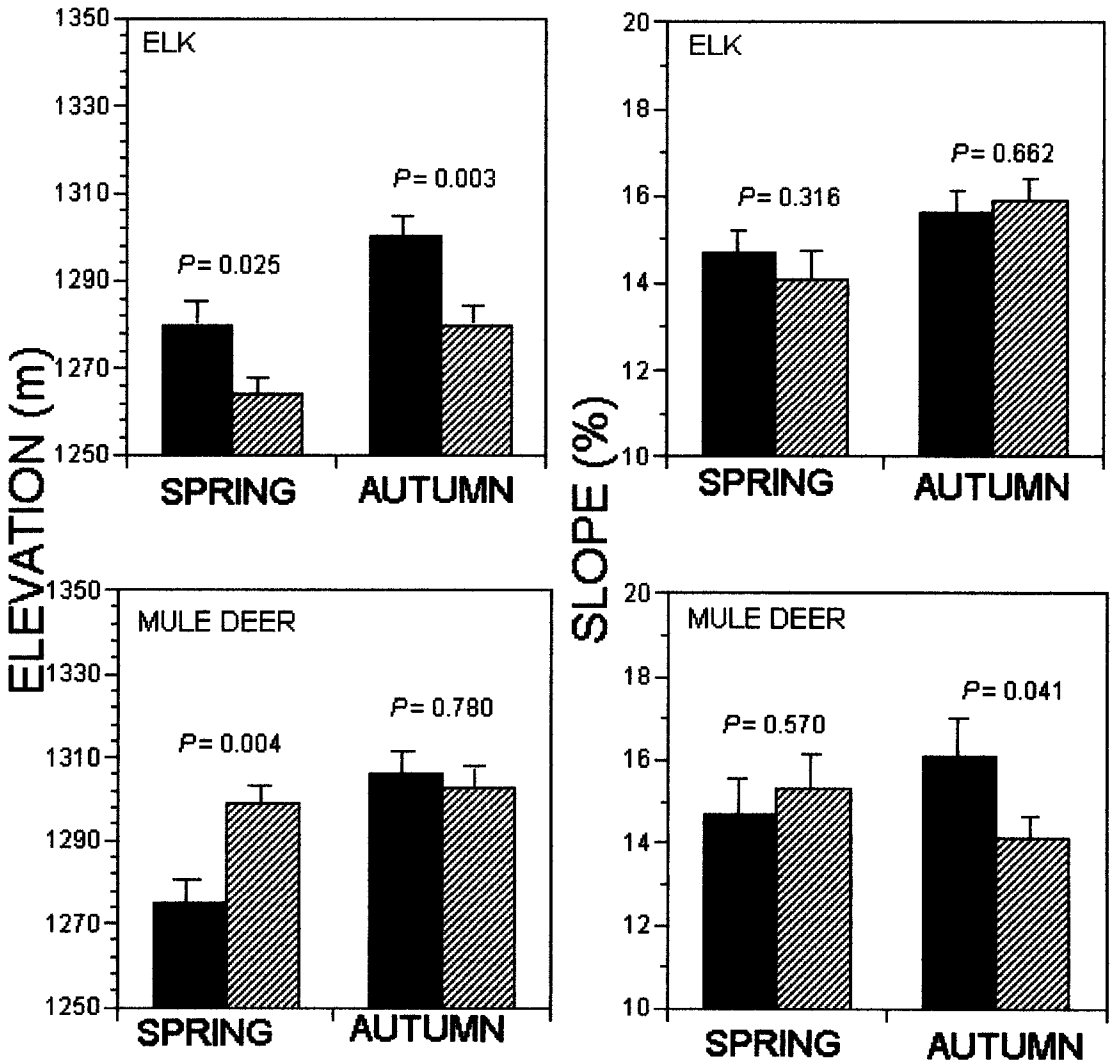

Figure 1.5. —Mean (± *SE*) seasonal use of elevation and slope by elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) in response cattle presence and absence on the Starkey Experimental Forest and Range, Oregon, 1993-1995. *P*-values are from ANOVA following significant treatment effects from MANOVAs (*Wilks' lambda P* < 0.05).

CHAPTER 2[2]

NICHE PARTITIONING AMONG MULE DEER, ELK, AND CATTLE: DO STABLE ISOTOPES REFLECT DIETARY NICHE?

Abstract: We examined dietary niches of mule deer (*Odocoileus hemionus* Linnaeus), North American elk (*Cervus elaphus* Linnaeus), and free-ranging cattle (*Bos taurus* Rafinesque); species that frequently co-occur in western North America. We tested the hypothesis that those 3 species would exhibit little overlap in diet and that mule deer, smallest in body size of the 3 species, would forage more selectively than either elk or cattle. We determined diet composition from microhistological analysis and used principal-components analysis to assess dietary niches. In addition to those conventional methods, we also assessed whether dietary overlap among those 3 ruminants would be reflected in stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) from fecal pellets. Principal component 1 represented a foraging axis based on plant classes, whereas principal component 2 represented a continuum from grazing to browsing, which revealed separation in means among 3 large herbivores. Similarly, $\delta^{13}C$ and $\delta^{15}N$ differed significantly among species, and indicated differences in moisture regimes within habitats, and types of forages used by those 3 ruminants. Contrary to our predictions, mule deer had the greatest variability in diets, and foraged on more xeric forages than did either elk or cattle. Stable isotopes

[2] K. M. Stewart, R. T. Bowyer, J. G. Kie, B. L. Dick, and M. Ben-David. 2003. Niche partitioning among mule deer, elk, and cattle: do stable isotopes reflect dietary niche? Écoscience 10:297-302.

elucidated differences in dietary niche among 3 ruminants that was not evident from dietary analysis alone.

Keywords: *Bos taurus*, cattle, *Cervus elaphus*, diets, $\delta^{13}C$, $\delta^{15}N$, North American elk, microhistological analysis, mule deer, niche, *Odocoileus hemionus*, stable isotopes

Introduction

Resource partitioning among species traditionally has been evaluated along 3 niche axes: spatial separation (including use of different habitats), temporal avoidance, and dietary differences (Keddy, 1989; Ben-David, Bowyer & Faro, 1996; Kronfeld-Schor et al., 2001; Stewart et al., 2002). Exploring niche separation among large herbivores along all 3 axes is often a formidable task, because those mammals occupy relatively large home ranges and exhibit broad dietary niches. Stewart et al., (2002) strongly inferred competition among mule deer (*Odocoileus hemionus* Linnaeus), North American elk (*Cervus elaphus* Linnaeus), and introduced cattle (*Bos taurus* Rafinesque), along 2 axes, spatial separation and temporal avoidance, using modern regression methods (Fox & Luo, 1996; Luo, Monamy & Fox, 1998). Stewart et al., (2002) reported high overlap in habitat use during summer, and postulated that this spatial distribution might result in low overlap on a dietary niche axis. High overlap on one niche axis typically is accompanied by avoidance on another axis where ecologically similar species co-exist (Kie & Bowyer, 1999; Krebs, Ryan & Charnov, 1974; MacArthur & Pianka, 1966)

Among ruminants, physiological and nutritional requirements differ in relation to body size (Jarman, 1974; Demment & Van Soest, 1985; Hoffman, 1985; Robbins, 1993;

Barboza & Bowyer, 2000, 2001). Interactions among different nutritional requirements, availability of forages, and occurrence of competitors help determine diet selection of individuals in community assemblages of ruminants (Anthony & Smith ,1977; Singer, 1979; Smith, 1987; Mower & Smith, 1989; Jenkins & Wright, 1988). Diets also may be constrained by mouth architecture, particularly incisor breadth (Illius & Gordon, 1987), which likewise increases with body mass (Spaeth et al., 2001).

Conventional methods for determining diet usually yield valuable information on dietary overlap. Nonetheless, recent studies demonstrated the utility of ratios of stable isotopes in exploring differences in diet composition for numerous species, including ruminants (Cormie & Schwarcz, 1994, 1996; Ben-David, Shochat & Adams, 2001). For example, isotope ratios for moose (*Alces alces* Gray) and caribou (Rangifer tarandus Hamilton-Smith) from Denali National Park and Preserve reflected diets of each species and indicated seasonal changes in foraging strategies and animal condition (Ben-David, Shochat & Adams, 2001); therefore, we restricted our analysis summer only to avoid effects of seasonal changes in forage availability.

In this study, we explored niche separation among mule deer, elk, and cattle and hypothesized that these 3 herbivores would exhibit low overlap in use of forages in summer (when the greatest spatial overlap among species occurred; Stewart et al. 2002). Further, we hypothesized that the smaller-bodied species, mule deer, would be more selective in their diets as indicated by less variability among individual diets and by use of higher-quality forages. Finally, we hypothesized that dietary differences among these 3 species would be reflected in their $\delta^{13}C$ and $\delta^{15}N$ signatures.

Study area and methods

We conducted research on the Starkey Experimental Forest and Range (hereafter, Starkey) of the United States Forest Service. Starkey (45° 12' N, 118° 3' W) is situated in the Blue Mountains of northeastern Oregon, USA, with elevations ranging from 1,120 to 1,500 m. Starkey encompasses 10,125 ha, and is surrounded by a 2.4-m high fence that prevents immigration or emigration of large herbivores (Rowland et al., 1997). Population size was approximately 500 adult female cattle (with young) in the main study area (7,762 ha) where feces were collected for cattle. We collected feces from mule deer and elk in the northeast study area (1,453 ha) and population sizes were 75 mule deer, and 130 elk in the as determined from stocking rate and helicopter censuses (Rowland et al., 1997; Stewart et al., 2002).

Both study areas consisted of 4 major habitats: (1) mesic forest with the overstory dominated by grand fir (*Abies grandis* [Dougl.] Forbes), and understory consisting of forbs and shrubs; (2) ponderosa pine (*Pinus ponderosa* Dougl.) forest, xeric community with the understory dominated by elk sedge (*Carex geyeri* Boott); (3) xeric grasslands dominated by a few grasses and forbs; and (4) logged forest, harvested during 1991-1992 (Rowland et al., 1998; Stewart et al., 2002).

We collected fresh (< 2 days old) fecal pellets opportunistically from mule deer (n = 28), elk (n = 27), and range cattle (n = 20) while sampling vegetation during summer (July-August) 1997. Cattle feces were collected from the main study area and feces from mule deer and elk were collected from the northeast study area. Habitats and forages

available were similar for main and northeast areas, and mule deer and elk were present in both areas. Feces were collected across large portions of the study areas to ensure that samples were representative of available habitats, and to minimize the possibility that the same individual was sampled repeatedly. Each fecal sample was analyzed for diet composition and for values of $\delta^{13}C$ and $\delta^{15}N$.

We analyzed feces for diet composition using microhistological analyses, conducted at Washington State University (B. Davitt, Pullman, Washington, USA). We used multivariate analyses of variance (MANOVA) with planned contrasts to test for differences in composition of forage classes among species (Neter et al., 1996). We used arcsine, square-root transformations to ensure additivity of treatment effects (Gilbert, 1973; Kie & Bowyer, 1999). We conducted principal-components analysis (PCA) based on the variance-covariance matrix to reduce dimensionality of those data (SAS Institute Inc., 1988; McGarigal, Cushman & Stafford, 2000). We plotted the mean with 95% confidence intervals as bivariate ellipses for the first 2 principal components to examine differences among herbivores.

Fecal samples were analyzed for ratios of stable isotopes of carbon and nitrogen following the methods of Ben David et al., (1998) and Ben David, Hanley & Schell, (1998). We used multi-response permutation procedures (MRPP; BLOSSOM, Slauson, Cade & Richards, 1991) to investigate differences among species in stable isotopes of carbon and nitrogen for fecal samples. MRPP are distribution-free statistics that rely on permutations of data based on randomization theory (Slauson, Cade, & Richards, 1991).

Results

Mule deer, elk, and cattle exhibited diverse diets as estimated from microhistological analyses of feces: mule deer (74 plant species); elk (80 plant species); and cattle (51 plant species). Mule deer consumed mostly sedges, but also ate about equal portions of grasses, forbs, conifers, and shrubs. Elk concentrated on forbs with some grasses and shrubs in their diets, whereas cattle fed principally upon grasses and sedges (Table 2.1). Diets of mule deer were highly variable: forbs ranged from 0 to 70%, and sedges from 0 to 88% of individual diets (Table 2.1). Diets of elk were generally less variable, although grasses ranged from 4 to 54% of diets; cattle diets had the lowest variability among forage classes (Table 2.1).

Significant differences occurred among species in use of forage classes (*Wilk's Lambda* $F_{10, 136}$; $p < 0.0001$). Pairwise comparisons among species demonstrated that cattle and mule deer differed in use of forage categories ($p < 0.05$) except forbs ($p = 0.075$); cattle and elk differed in use of forage classes ($p < 0.05$) except for small amounts of conifers ($p = 0.92$). Mule deer and elk differed in use of forage classes ($p < 0.01$) except for other foods ($p = 0.97$; Table 2.1).

We reduced dimensionality of data from 6 variables indicating forage classes (forbs, grasses, sedges, shrubs, and conifers) to 2 principal components that explained 70% of the variation in those variables. Means with 95% confidence intervals indicated separation of groups of principal-component scores based upon forage classes dominant in the fecal pellets of the 3 herbivores (Figure 2.1). We considered principal component 1 (39%) a forage-class axis ranging from sedges (negative loadings) to forbs (positive

loadings); diets dominated by graminoids (> 50%) loaded slightly negative (0-1.5), and those containing mostly forbs (> 20%) loaded more positively (1-2; Figure 2.1). Principal component 2 (31%) ostensibly represented a continuum from grazing (negative loadings) to browsing (positive loadings; Figure 2.1). Diets that reflected a grazing strategy (dominated by grasses) loaded negatively for principal component 2, whereas those diets dominated by shrubs and conifers, which represented a browsing strategy, loaded strongly positive on that same axis (PC2). Moreover, 95% confidence ellipses for centroids, calculated from scores for principal components 1 and 2, clearly separated mule deer, elk, and cattle on those 2 axes representing forage classes (PC1) and feeding strategies (PC2; Figure 2.1).

Stable isotope ratios indicated high variability in diet for all 3 herbivores with mule deer exhibiting the greatest variability (Table 2.1, Figure 2.2). MRPP indicated significant ($p < 0.01$) differences among mule deer, elk, and cattle for isotope ratios of both $\delta^{15}N$ and $\delta^{13}C$. Moreover, pairwise comparisons among species of ratios of stable isotopes revealed significant differences between mule deer and cattle ($p < 0.001$), mule deer and elk ($p < 0.001$), and elk and cattle ($p = 0.004$).

Discussion

We hypothesized that mule deer, elk, and cattle would exhibit little overlap in diets. Indeed, both dietary and stable isotope analyses indicated complete separation of means in diets among those 3 species when both axes were considered together (Figures 2.1 & 2.2). Stewart et al., (2002) reported significant overlap in habitat use among these 3 large herbivores during summer; thus, mule deer, elk, and cattle used similar habitats

while diverging strongly in diets. Principal component 2 clearly separated mean diets of these 3 ruminants by foraging strategy. Despite diets containing large amounts of sedges, mule deer followed a browsing strategy, elk were intermediate or mixed-feeders, and cattle were grazers during summer.

We predicted that small-bodied mule deer would exhibit a narrower dietary niche with forage of higher quality than either larger-bodied elk or cattle (Mackie, 1970; Schoener, 1971; Demment & Van Soest, 1985; Robbins, 1993; Kie & Bowyer, 1999). In contrast to both predictions, mule deer exhibited greater variability in dietary niche than elk or cattle (Figures 2.1 & 2.2). Sedges dominated diets of mule deer on average, but varied greatly from 0 to 88% of individual diets (Table 2.1). Nonetheless, mule deer consumed numerous forbs, shrubs, and conifers, indicating that deer were opportunistic feeders compared with elk and cattle, which foraged primarily on forbs and grasses, respectively. This result was somewhat unexpected and may indicate that mule deer foraged on plants of lower quality than either elk or cattle. Perhaps, by increasing variability in the diets by feeding opportunistically, mule deer increased overall diet quality. More research into this question, however, is required.

We hypothesized these 3 large herbivores would differ in stable-isotope signatures and that divergence in those ratios would reflect differences in diets among mule deer, elk, and cattle. Indeed, those 3 species of ungulates differed significantly on both $\delta^{13}C$ and $\delta^{15}N$ axes together, further indicating separation in means on a dietary niche axis (Figures 2.1 & 2.2). Although differences in isotopic ratios among the 3 species were not large, feces of mule deer were significantly depleted in $\delta^{15}N$ and

enriched in $\delta^{13}C$ compared with either elk or cattle (Figure 2.2). Depletion of $\delta^{15}N$ in feces of mule deer, in concert with enrichment of $\delta^{13}C$, likely resulted from consumption of forages occurring in more xeric habitats dominated by sedges. Enrichment in $\delta^{13}C$ has been reported as a result of higher soil temperature or water stress in plants (Lipp et al., 1991; Michelsen et al., 1996; Panek & Waring, 1997; Barber, Juday & Finney, 2000), an outcome consistent with xeric forages used by mule deer. C4 plants are often isotopically heavier in $\delta^{13}C$ than C3 plants (Gearing 1991). Thus, consumption of C4 plants may affect values of $\delta^{13}C$ in feces, but C4 plants were not present on either study area or in herbivore diets we sampled. Indeed, other studies have noted that mule deer occupied xeric habitats, characterized by ponderosa pine overstory with an understory dominated by elk sedge (*Carex geyeri*), than those habitats used by elk or cattle (Johnson & Clausnitzer, 1992; Johnson et al., 2000; Coe et al., 2001, Stewart et al., 2002).

Elk and cattle separated on the $\delta^{15}N$ axis, but not the $\delta^{13}C$ axis (Figure 2.2). Such differences in values of $\delta^{15}N$ probably reflected reliance of elk on forbs (including legumes), and cattle on grasses. Elk likely fed more on leguminous forbs that rely on atmospheric N_2-fixation resulting in $\delta^{15}N$ values near 0 in feces of elk, which is consistent with signatures of plant species that fix atmospheric nitrogen (Nadelhoffer & Fry, 1994; Ben-David et al., 1998).

Comparisons of 95% confidence intervals for means of PC1 scores from dietary analysis with ratios of stable isotopes highlight the differing results obtained by those 2 methods. PC1 indicated strong overlap of forage classes between mule deer and cattle, but differences in between cattle and elk (Figure 2.1). Stable isotopes indicated the

opposite (Figure 2.2). Although elk and cattle separated on the $\delta^{15}N$ axis, significant overlap occurred in the $\delta^{13}C$ axis, precluding the interpretation that cattle also utilized more xeric types of forages, similar to diets of mule deer. Stewart et al. (2002) frequently observed cattle at low elevations on shallow slopes with mesic vegetation. Thus, isotopic data may reflect differences in use of forages between cattle and mule deer more clearly than dietary data, because of differences in moisture conditions of those habitats and types of forages contained therein. Stable isotopes may provide an added dimension to understanding dietary partitioning among large herbivores that inhabit landscapes consisting of diverse habitats. Nonetheless, stable isotopes may not reflect differences in habitat use between cattle and elk as efficiently as for mule deer, because of similar moisture regimes and more mesic conditions of those forages consumed.

Niche separation is traditionally evaluated along spatial, temporal, and dietary axes, and conclusions about niche dynamics from a single axis alone may lead to misinterpretation of results (Keddy, 1989; Ben-David, Bowyer & Faro, 1996; Kronfeld-Schor et al., 2001). Although mule deer, elk, and cattle were reported to overlap in use of habitats (Stewart et al. 2002), our examination of diets indicated strong partitioning of dietary niche and some separation of habitats related to moisture regimes, with mule deer using more xeric habitats than either elk or cattle. Contrary to our prediction, mule deer exhibited the greatest variability in dietary niche and used lower-quality forages occurring in xeric habitats. Although mule deer consumed large amounts of sedges, they continued to follow a browsing strategy. Stable isotope analysis was useful in determining moisture regimes of forages eaten by ungulate species, and

indicated some partitioning of habitats in addition to forages, which was not evident from simply examining diets. Thus, we hypothesize that the arrangement of forages in a heterogeneous landscape (sensu Kie et al., 2002) may be as important as body size in determining dietary niche; more research on this complex topic is needed.

Acknowledgements

We appreciate the assistance of Starkey project personnel. F. Weckerly, M. Vavra, J. Rachlow, S. Finholdt, and R. W. Ruess provided helpful comments on the manuscript. This study was funded by the United States Forest Service and the Institute of Arctic Biology at the University of Alaska Fairbanks. This manuscript is Rob and Bessie Welder Foundation contribution number 399.

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Table 2.1. Descriptive statistics for diet composition (%) of feces of cattle (n = 20), mule deer (n = 28) and elk (n = 27) during summer 1997 on the Starkey Experimental Forest and Range, northeastern, Oregon, USA.

Species and forage class	$\bar{X}$	SD	Minimum	Maximum
Mule Deer				
Conifers	8.4	13.13	0	56.2
Forbs	14.4	21.33	0	70.4
Grasses	16.6	8.55	3.5	33.3
Sedges	47.4	29.90	0	88.0
Shrubs	8.5	9.51	0	40.9
Other foods	4.8	6.72	0	34.2
Elk				
Conifers	0.8	1.28	0	4.2
Forbs	44.7	11.07	24.9	46.7
Grasses	31.2	10.80	4.4	53.8
Sedges	11.7	6.16	1.5	26.4
Shrubs	6.9	4.67	0	18.2
Other foods	4.8	3.29	0	12.7

Table 2.1. Continued

Species and forage class	$\overline{X}$	SD	Minimum	Maximum
Cattle				
Conifers	0.6	0.68	0	2.1
Forbs	6.6	3.26	0.7	11.3
Grasses	53.4	12.84	23.8	53.0
Sedges	36.6	12.06	19.8	50.9
Shrubs	1.5	1.94	0	6.9
Other foods	1.4	1.50	0	5.8

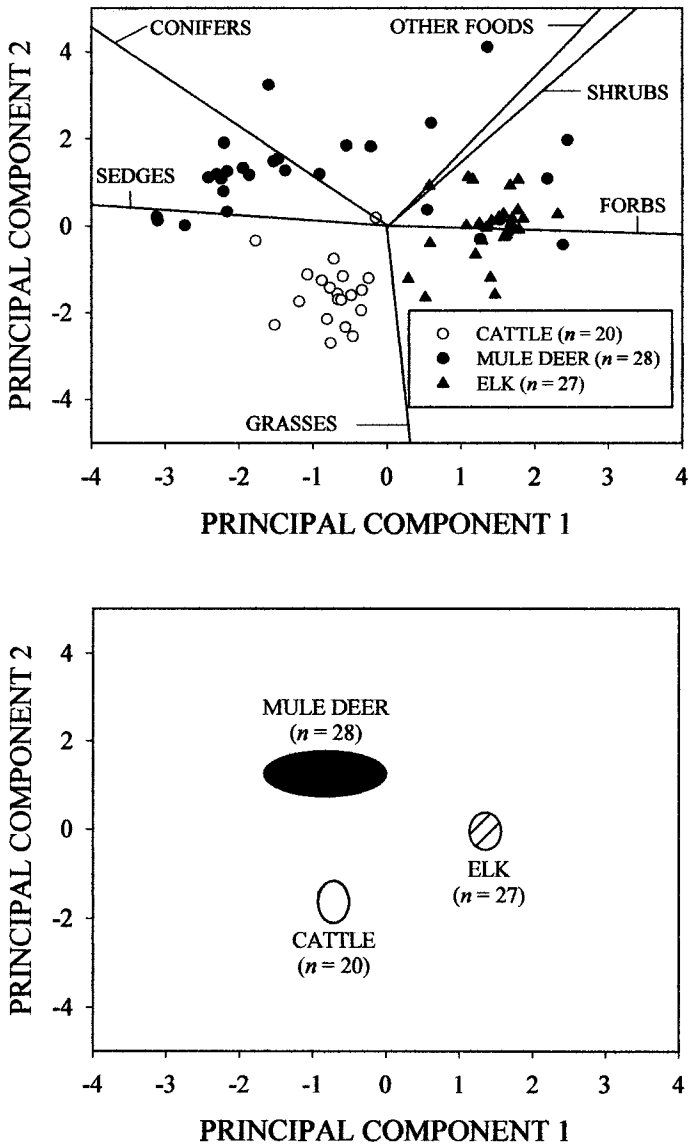

Figure 2.1. Results of principal components analysis (PCA) on forage classes determined from microhistological analysis of feces of cattle, mule deer, and elk with plots of principal components 1 and 2 (70% of variation explained). The top graph is a biplot scatter of principal component scores with loadings for forage classes indicated by vectors. Principal component 1 is a forage type axis, whereas principal component 2 represents a browsing versus grazing continuum. The bottom graph contains 95% confidence intervals for centroids calculated from principal component scores for cattle, mule deer, and elk during summer on the Starkey Experimental Forest and Range, northeastern Oregon, USA, 1997.

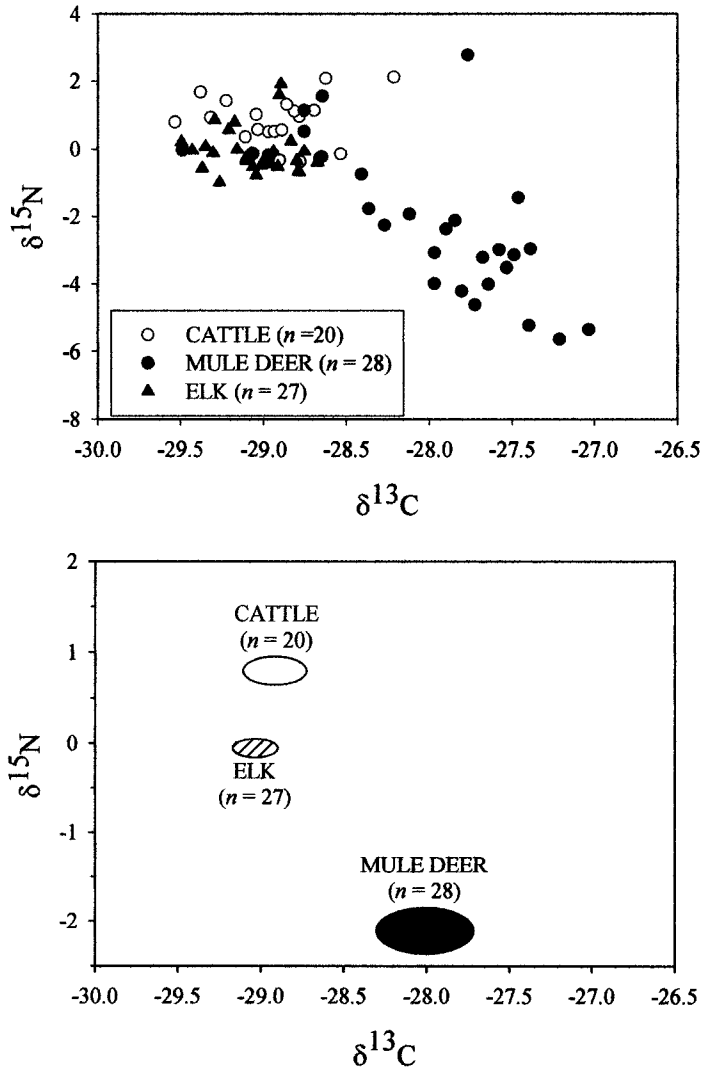

Figure 2.2. Results of stable isotope analyses from feces of cattle, mule deer, and elk. The top graph is a scatter plot of $\delta^{13}C$ and $\delta^{15}N$ ratios. The ellipses in the bottom graph are 95% confidence intervals for centroids calculated from stable isotope ratios of cattle, mule deer, and elk during summer on the Starkey Experimental Forest and Range, northeastern Oregon, USA, 1997. Values of $\delta^{13}C$ are derived from comparison of the ratio of the heavy (^{13}C) and light (^{12}C) isotopes in the sample with the ratio of those 2 isotopes in a standard (PDB limestone) using the equation $\delta^{13}C = \{[(^{13}C / {}^{12}C)_{sample} / (^{13}C / {}^{12}C)_{standard}] - 1\} \times 10^3$. Because PDB limestone is highly enriched in ^{13}C relative to most biological samples, values of $\delta^{13}C$ are usually negative. Values of $\delta^{15}N$ are calculated in a similar manner. The value of the standard, atmospheric nitrogen, is set by convention to 0 (Nadelhoffer & Fry, 1994).

CHAPTER 3[3]

DENSITY-DEPENDENT EFFECTS ON PHYSICAL CONDITION AND REPRODUCTION IN NORTH AMERICAN ELK: AN EXPERIMENTAL TEST

Abstract Density dependence plays a key role in life-history characteristics and population ecology of large, herbivorous mammals. We designed a manipulative experiment to test hypotheses relating effects of density-dependent mechanisms on physical condition and fecundity of female North American elk (*Cervus elaphus*). We hypothesized that if density-dependent effects were manifested principally through intraspecific competition, body condition and fecundity of females would be lower in an area of high population density than in a low-density area.

Our manipulative experiment indicated that density-dependent feedbacks affected condition and reproduction of adult female elk. Age-specific pregnancy rates were lower in the high-density area, although there were no differences in age at first reproduction between areas. Age-specific rates of pregnancy began to diverge at 2 years of age between the two populations and peaked at 6-8 years old. Pregnancy rates were most affected by body condition and mass, although age had a negative effect on pregnancy of individuals, probably because of senescence in older age classes. Our results indicated that while holding effects of winter constant, population density and density-dependent mechanisms had a much greater effect on physical condition and fecundity than density-independent factors (e.g., precipitation and temperature).

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[3] K. M. Stewart, R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. In Review. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. Oecologia

Moreover, our results demonstrated effects of differing nutrition resulting from population density during summer on body condition and reproduction. Thus, summer is a critical period for accumulation of body stores to buffer animals against winter; more emphasis should be placed on the role of spring and summer nutrition on population regulation in large, northern herbivores.

Key words: body mass · body condition · *Cervus elaphus* · lactation · pregnancy · reproduction

Introduction

Detecting density dependence is neither simple nor straightforward (McCullough 1990; Kie et al. 2003). Density-dependent processes for ungulates often interact with other variables including predation, harvest, and genetics, as well as density independent factors such as climate—those interactions can make such processes difficult to document (McCullough 1979, 1990; Sand 1996; Crête and Curtois 1997; Sæther 1997; White and Bartmann 1997; Post and Stenseth 1998; Bowyer et al. 1999; Aanes et al. 2000; Coulson et al. 2000). Density dependence has been investigated, with varying results, in birds (Sedinger et al. 2001; Schmutz and Laing 2002; Wang et al. 2002; Both and Visser 2003; Elmberg et al. 2003), small mammals (Aars and Ims 2002, Lima et al. 2002, Selas et al. 2002), carnivorous mammals (Fryxell et al. 1999; Macdonald et al. 2002), and large, herbivorous mammals (McCullough 1979; Kie et al. 1983; Kie and

White 1985; Skogland 1985; Bowyer et al. 1999; Mysterud et al. 2000; Sæther et al. 2002; Toigo et al. 2002).

Most aspects of the ecology of large mammals are influenced by density-dependent processes (McCullough 1979, 1999; Fowler 1981; Gaillard et al. 2000; Kie et al. 2003 for reviews). Thus, large mammals offer a quintessential model for studying density dependence because of their life-history strategies, including strong competitive ability, large body size, long lifespan, low reproductive rate, and high maternal investment (McCullough 1979; Clutton-Brock 1987; Rachlow and Bowyer 1994; Gaillard et al. 2000). Although numerous studies of large herbivores have demonstrated the role that density dependence plays in the dynamics and regulation of populations (Klein 1968; Caughley 1970; Kie and White 1985; Skogland 1985; Clutton-Brock et al. 1987; Boyce 1989; Bartmann et al. 1992; Sand 1996; Singer et al. 1997; Kie and Bowyer 1999), others have failed to detect those processes (Banasiak 1961; Gasaway et al. 1983; Mackie 1990). Density dependence has been difficult to document and most studies attempting to examine density-dependent mechanisms of large herbivores make comparisons across too narrow a breadth of densities with respect to ecological carrying capacity (K) or too short a time span to detect changes in fecundity, recruitment, or survival and, as a result, often fail to detect those processes (McCullough 1990; Kie et al. 2003). Research substantiating the importance of density-dependent mechanisms in ungulate populations typically has come from long-term studies in which populations varied markedly in size with respect to K, and appropriate vital rates for populations were collected (McCullough 1979; Clutton-Brock et al. 1987; Gaillard et al. 2000). Such a

design, however, cannot sort stochastic effects that occur among years from influences of density dependence (White and Bartmann 1997). Moreover, comparing densities among populations to evaluate parameters such as recruitment or survival is meaningless without knowledge of where those populations are with respect to *K* (McCullough 1979; Weixelman et al. 1998; Bowyer et al. 1999; Kie et al. 2003). Few studies have experimentally tested effects of high- and low-population density of large, herbivorous mammals simultaneously in the same ecosystem, because of the difficulty of performing manipulative experiments on those large mammals (McCullough 1979).

Forage availability during winter often is thought to be most critical for regulating populations of large mammals; estimates of *K* and habitat improvements typically are focused on winter ranges (Banasiak 1961; Mackie 1990; Raedeke et al. 2002). Conversely, other studies report that nutrition during summer is critical for building body reserves to sustain animals during winter (Mautz 1978; McCullough and Ullrey 1983; Cook et al. 2003). Pederson and Harper (1978) noted that differences in productivity of two herds of mule deer (*Odocoileus hemionus*) resulted from differences in forage availability and quality on summer ranges. Moreover, Teer et al. (1965) reported variation in counts of corpora lutea with changes in population density of white-tailed deer (*Odocoileus virginianus*), which would not have occurred if forage in spring and summer were not in short supply. Among temperate and arctic ungulates, nutritional requirements during winter cannot be met because of low-quality forage; consequently, winter nutrition is dependent on catabolism of body stores (Mautz 1978; McCullough and Ullrey 1983; Schwartz et al. 1988b; Parker et al. 1999). Schwartz et al. (1988b) reported

that moose (*Alces alces*) consuming ad libitum amounts of winter browse were in negative energy balance and noted that the length of time an animal could survive on winter range was a function of energy stores accumulated in other seasons and rate of their depletion. Thus, density-dependent effects on reproduction and physical condition occur via differences in summer nutrition, as well as rates of winter depletion of those resources. Nonetheless, few critical tests of the role of summer range on density-dependent processes exist because of interactions between seasons resulting from depletion of body reserves accrued in summer during winter.

We designed a manipulative experiment to examine effects of density-dependent processes in North American elk (*Cervus elaphus*) at high- (near *K*) and low-population (below maximum sustained yield, MSY) densities, simultaneously in the same system. We hypothesized that differences in body condition and reproduction between high and low densities of elk would result from density-dependent processes (Table 3.1). If those density-dependent effects were manifested principally through intraspecific competition, we predicted that body condition and pregnancy rates of adult females would be lower in the high-density population than for the population at low density (Table 3.1). We also hypothesized that effects of density dependence would be exhibited by differences in nutrition obtained during spring, summer, and autumn, while experimentally holding effects of winter nutrition constant. Although such data would need to be collected across a wide range of densities and include information on survivorship of young (Table 3.1) to fit a recruitment curve (sensu McCullough 1979), our experimental manipulation

of elk density provides a critical test of whether density dependence in reproduction occurs for this large mammal.

Methods

Study Area

We conducted research from 1998 through 2001 on the Starkey Experimental Forest and Range (hereafter, Starkey) of the United States Forest Service. Starkey (45° 12' N, 118° 3' W) is situated in the Blue Mountains of northeastern Oregon and southeastern Washington, USA, and is located 35 km southwest of La Grande, Oregon, USA. Elevations range from 1,120 to 1,500 m. This site supports a mosaic of forests and grasslands, which are typical summer ranges for elk in the Blue Mountains (Rowland et al. 1997; Johnson et al. 2000). Starkey encompasses 10,125 ha, and since 1987 has been surrounded by a 2.4-m fence that prevents immigration or emigration of large herbivores, including migration to traditional winter ranges (Rowland et al. 1997). We restricted collection of data to the northeast experimental area on Starkey, which encompassed 1,452 ha, and was separated from the remainder of the study area by the same type of fence (Stewart et al. 2002). The northeast study area was divided into 2 pastures, east (842 ha) and west (610 ha), to accommodate experimental comparisons of population densities of elk. We divided the northeast area to ensure that habitats were in equal proportion in the east and west areas (Stewart et al. 2002).

The northeast area consisted of four major habitats: (1) mesic forest dominated by grand fir (*Abies grandis*); (2) xeric forest characterized by Ponderosa pine (*Pinus*

ponderosa); (3) xeric grassland dominated by a few grasses and forbs, such as onespike oatgrass (*Danthonia unispicata*), Idaho fescue (*Festuca idahoensis*) and low gumweed (*Grindelia nana*); and (4) logged forest harvested in 1991-1992, and then seeded with rhizomatous grasses including bluegrass (*Poa* sp.—Stewart et al. 2002).

Eastern Oregon is host to a suite of large predators including, black bears (*Ursus americanus*), mountain lions (*Puma concolor*), bobcats (*Lynx rufus*) and coyotes (*Canis latrans*; Verts and Carraway 1998). These predators occur infrequently on Starkey and no effort was made to control predators on our study areas.

Experimental Design and Statistical Analyses

Elk populations were at moderate density on the study area during 1998 (east area 4.51 elk/km^2; west area 5.41 elk/km^2). During 1999, we began an experiment to examine effects of population density by comparing a population at high density, which was randomly assigned to the east area, and a low-density population in the west area. We selected 4.0 elk/km^2 for the low-density population and 20.0 elk/km^2 for the high-density population based on earlier work on Starkey (Rowland et al. 1997). Our high-density population represented a high concentration of animals; however, nonhunted populations of elk have been reported to attain densities as high as 33 elk/km^2 (Houston 1982; Hobbs et al. 1996). Moreover, Hobbs et al. (1996) used 31 elk/km^2 for their high-density treatment in an experiment examining resource competition between cattle and elk. We were constrained in the size of our low-density population by the need to have an adequate sample of animals in the low-density area, which included about 30 elk. The

experiment was begun during May 1999. Within 1 month of beginning the experiment, however, a gate was left open between study areas, resulting in movement of elk from the high- to the low-density population. Thus our low-density population for that year was 6.6 elk/km^2 and the high-density population 10.8 elk/km^2. During the final 2 years of study (2000 and 2001), we maintained a high-density population at 20.1 elk/km^2 and low-density population of 4.1 elk/km^2.

Elk no longer migrate from the study area to traditional winter ranges because of the fence, and are maintained throughout winter in a holding area in which they are fed a maintenance diet of alfalfa hay (Rowland et al. 1997). Elk from both population densities are held together and fed the same diet on the feedground during winter. Thus, analyses of effects of density dependence in this study are related to nutrition during late spring, summer, and autumn, because feeding in winter was constant for the two population densities, and elk experienced identical winter weather conditions. Elk were released from the winter feeding area during late April. We were unable to keep individuals in the same population each year, because of the limited area for holding animals on the winter feedground. Therefore, the experiment was reset each year. Accordingly, we subset those data by randomly selecting 1 year of data for each individual and eliminating that individual from other years; consequently, each individual elk was represented once in statistical analyses,.

As elk entered the feedground during winter, they were captured in a small pasture and moved via a system of alleys through the handling facility for collection of data on individual animals (Rowland et al. 1997). Adult male elk with antlers were not

handled, but released directly onto the winter feedground. Yearlings, young (< 1 year old), and adult females (≥ 2 years old) were processed through the handling facility. Each animal was identified by ear tags with unique numbers, or previously unknown animals were marked with new ear tags. Animals that were handled initially as adults were recorded as an adult age class—their exact age was unknown. Conversely, animals handled initially as young or yearlings were recorded as known-age individuals. We restricted our analyses on reproduction and body condition to include only known-age individuals from each of our study areas. Although we present data for age of elk in whole years, those individuals were recorded as they entered the winter feedground in November or December, and consequently were 7-8 months older than indicated.

Body mass was determined for each individual with a digital scale to the nearest 1 kg. Blood was collected from the jugular veins of adult and yearling females, and serum was analyzed (Bio Tracking, Moscow, Idaho, USA) for pregnancy-specific protein B to determine pregnancy rates (Noyes et al. 1997; Russell et al. 1998; Keech et al. 2000). Depth of maximum rumpfat (maxfat) was determined as an index of body condition for adult and yearling female elk via ultrasonography (Stephenson et al. 1993; Keech et al. 1998; Stephenson et al. 1998; Keech et al. 2000). Data on rumpfat were collected at the midpoint between the illium and ischial tuberosity (midfat), rather than maximum fat levels (maxfat) during 1998; however, from 1999 through 2001 we collected data for both mid and maximum depth of rumpfat for yearling and adult females. We used linear regression to develop equations to convert midfat to maximum depth of rumpfat for 1998, to compare maximum fat levels collected on all yearling and adult female elk (Cook et al.

2001). The regression equation was: maxfat = 0.0265 + 1.2409midfat ($r^2 = 0.939$, $P < 0.0001$). All further analyses of depth of rumpfat were performed on maximum levels of fat for 1999-2001 and the converted values of maxfat for 1998 only.

We collected data on temperature and precipitation from a National Atmospheric Deposition Program (NADP) weather station located on Starkey. We determined annual and seasonal precipitation based on periods defined by Stewart et al. (2002): winter (November-March); spring (April-June); summer (July-September); and autumn (October). We calculated number of degree days >5°C (number of degrees that the mean daily temperature was >5°C, summed across all days; Bowyer et al. 1998). This variable was selected because it provided an index of growth for plants in seasonal environments (Chapin 1983; Bowyer et al. 1998).

We compared population density for each year against maximal depth of rumpfat (an index of body condition) and proportion of adult females and yearlings pregnant in each area using one-tailed Spearman rank correlations (r_s) (Neter et al. 1990). We selected one-tailed tests because the direction of the relationship between population density, physical condition, and reproduction was known (Kie et al. 2003). Spearman rank correlations are nonparametric and make no assumptions concerning the shape of the relationships between variables (Zar 1999, Bowyer et al. 2001). We also tested for density-independent factors affecting body condition using one-tailed Spearman rank correlations to compare annual precipitation and temperature for each year of study versus maximal depth of rumpfat for each population density. We also tested for

interactions between annual precipitation and population density, as well as temperature and annual precipitation on body condition of female elk.

We examined growth of elk by fitting the von Bertlanffy equation for sigmoidal growth of body mass against age of elk (Ricker 1979; Zullinger et al. 1984; Spaeth et al. 2001) using nonlinear regression (Proc NLIN, SAS Inst. 2001). We used multivariate analysis of covariance (MANCOVA) to examine indices of body condition of individual adult female elk between high and low population densities in1999-2001, years during which our population densities were most disparate. We followed multivariate analyses with individual analysis of covariance (ANCOVA) for each of the body-condition indices. Because populations of large herbivores are strongly age-structured, that variable is an important factor when examining differences in body mass (Kie et al. 1983; Gaillard et al, 2000; Pettorelli et al. 2001); accordingly, age was used as the covariate in those analyses.

We calculated proportion of elk pregnant for all known-aged individuals for high and low-density populations from 1999 to 2001, with each individual elk represented once in analyses to prevent inflation of sample size associated with numerous samples from particular individuals. We used simple linear regression, weighted by the number of animals pregnant for each age, to examine the relationship between pregnancy rates and age for high- and low-density populations (Neter et al. 1990). We compared nonlinear regressions for the two populations using the F-test to examine regression coefficients (Neter et al. 1990). We then compared elevations of those regression parabolas to determine if the proportion of elk pregnant in the high-density population

was lower than that of the low-density population using the one-tailed *t*-test for comparison of elevations of regression lines (Zar 1999).

We employed stepwise logistic regression ($\alpha = 0.15$ to enter, 0.10 to remain) to examine effects of body condition, age, environmental variables (temperature and precipitation), and previous reproduction on pregnancy of individual elk following the mating season. Our dependent variable was pregnancy (1 = pregnant, 0 = not pregnant) and independent variables included: age (years), body mass (kg), rumpfat (mm), lactational status (1=lactating, and 0=not lactating), precipitation (cm), and temperature (degree days). Lactational status, measured during late autumn or early winter, was used to index effects of reproduction during the previous year on reproductive effort for the current year. We used a Hosmer and Lemshow goodness-of-fit test to evaluate aptness of the logistic model; odds ratios, *P*-values, and Akaike Information Criterion (AIC) were used to select the best logistic model.

Results

During 1998, elk in both study areas were maintained at moderate population densities and exhibited similar pregnancy rates; sample sizes were similar between study sites (Table 3.2). Our manipulation of population density began in 1999; however, our target population densities were not achieved until we further manipulated densities of elk during 2000-2001 (Table 3.2). We achieved five-fold differences in density during 2000-2001, where the low-density population consisted of 4.1 elk/km^2 and the high-density area was 20.1 elk/km^2 (Table 3.2), variation sufficient to obtain a critical test

of the role of density dependence on physical condition and reproduction in elk.

Proportion of females pregnant was negatively related to population density across 3 years (1999 to 2001) of our density manipulation (Figure 3.1). Fewer females became pregnant as population density increased. Body condition of adult and yearling females was negatively correlated with population density; females in the high-density area had poorer body condition than those in the low-density area (Figure 3.1). Annual precipitation (cm) did not affect body condition of adult females significantly ($r_s = 0.395$, $P = 0.332$); temperature (degree days) also did not affect body condition of female elk ($r_s = 0.119$, $P = 0.778$). No significant interaction occurred between precipitation and population density ($P = 0.113$) or temperature and precipitation ($P = 0.212$) on body condition of elk.

We observed an asymptotic relationship between body mass (kg) and age (years), indicating that age-specific growth of female elk followed a von Bertalanffy growth curve (Figure 3.2). Moreover, that curve indicated that age was an important factor when examining differences in body mass of individual animals. When age was included as a covariate, body condition of adult female elk was lower in the high-density than in the low-density area, but body mass of individuals did not differ between treatments (Table 3.3).

We observed a parabolic relationship between age and pregnancy rates of female elk on low- and high-density areas, with lower pregnancy rates at young and older ages (Figure 3.3). The greatest proportion of females pregnant occurred at 6 years of age for the high-density population and 7 to 8 years in the low density population; no significant

difference in the overall shape of curves occurred ($P > 0.05$; Fig. 3). Nevertheless, elevation of the regression parabola of the low-density population was greater than that of the high-density population ($P < 0.05$).

Our logistic models indicated that age, body mass, and maximal depth of rumpfat affected pregnancy of adult and yearling female elk (Table 3.4). The overriding factor affecting current-year reproduction was maximal depth of rumpfat, as indicated by odds ratios >12 times that of other variables (Table 3.4). Body mass and age were progressively less influential in affecting reproduction (Table 3.4).

Discussion

Density-dependent mechanisms are mediated through intraspecific competition, via per capita availability of food, and the subsequent influence of nutrition on reproduction and successful recruitment of young into the population (Simkin 1974; McCullough 1979; Sæther and Haagenrud 1983; Schwartz and Hundertmark, 1993; Keech et al. 2000). We predicted that density-dependent effects would be evidenced by differences in body condition and pregnancy rates of females between our manipulated populations of elk. Indeed, our results supported those predictions, and indicated that elk at high population density were much lower in physical condition and had lower proportion of females pregnant than elk maintained at low density (Fig. 3.1, Table 3.3). Adult female elk in Yellowstone National Park exhibited density-dependent effects on fertility and survivorship (Taper and Gogan 2002). Moreover, Lubow et al. (2002) reported strong density-dependent effects on recruitment and survival of juvenile elk as

population density approached *K*. Our results are consistent with other data on effects of population density on body condition in ungulates; females in poorer physical condition are less likely to reproduce (Robinette and Gashwiler 1950; Schladweiler and Stevens 1973; McCullough 1979; Adamczewski et al. 1997). Nonetheless, results of previous research include effects of both winter and summer conditions.

When we examined pregnancy rates between populations by age, we observed no differences in reproduction among yearlings, which was low or nonexistent in both study areas (Figure 3.3). At 2 years of age, however, pregnancy rates between the two populations began to diverge (Figure 3.3). Indeed, pregnancy rates among prime-aged (ages 4-9) elk were much lower in the high-density area compared with the low-density area—the greatest difference between densities was between 6 and 8 years old (Figures 3.1 and 3.3). Numerous studies have reported density dependence in adult fecundity and increasing age at first reproduction for large herbivores (Schladweiler and Stevens 1973; McCullough 1979; Kie and White 1985; Van Vuren and Bray 1986; Clutton-Brock et al. 1987; Houston and Stevens 1988; Kirkpatrick and Turner 1991). Our low-density population may not have been sufficiently low for yearlings to obtain sufficient resources and, hence, the improved physical condition necessary to initiate reproduction. We note, however, that we were limited to a moderate density by the necessity of obtaining an adequate sample for comparison. Moreover, changes in body mass with age fitted an asymptotic distribution, with adult body mass attained at about 2 years of age for females (Figure 3.2). Those growth curves did not differ among populations; reproduction of yearlings would likely require a critical body mass necessary to begin reproduction at a

younger age in the low-density population (sensu Cameron and Ver Hoef 1994). This outcome is not surprising because elk were not placed in high or low-density areas consistently and winter conditions were identical for all animals.

Twinning rates in moose are highly correlated with decreasing age at first reproduction (Keech et al. 2000; Boer 1992), and numerous studies have examined changes in litter size with concurrent changes in population density (Kie and White 1985; Gaillard et al. 2000). Elk rarely have more than one offspring (Bubenik 1982); thus, we could not examine differences in litter size between populations. Elk > 9 years of age began to exhibit senescence in pregnancy in the high-density population, although sample sizes for those age classes were low or nonexistent in the low—density population–this outcome needs further investigation (Figure 3.3). Nonetheless, senescence in reproduction has been reported for individual cervids in "old" age classes (Gaillard et al. 2000; Ericsson et al. 2001; Mysterud et al. 2001; Loison et al. 2002). Loison et al. (2002) noted decreasing survival of both sexes of ungulates >8 years of age; although onset of senescence in reproduction was 12 years of age in moose (Ericsson et al. 2001) and 20 years in female red deer in Norway (Mysterud et al. 2001).

We used logistic regression to examine factors that affected pregnancy among individual female elk. Because feedback processes associated with density dependence are mediated through nutrition, those individuals in populations near *K* tend to be in poor physical condition (McCullough 1979; Kie et al. 1983; Kie et al. 2003). Such animals typically are on a low nutritional plane, and often exhibit low rates of reproduction, delayed reproduction, and low survivorship (McCullough 1979; Kie et al. 1980; Skogland

1984; Bowyer et al. 1999; Kie et al. 2003). Moreover, intraspecific competition for resources may force adult females to make tradeoffs between parental investment in current offspring and future reproductive efforts (McCullough 1979; Clutton-Brock 1984). Factors affecting pregnancy among individual female elk in our study included age, and physical condition (body mass and depth of rumpfat; Table 3.4). Moreover, our examination of parameters that affected pregnancy rates, including previous reproductive efforts, indicated that variables that contributed most strongly to reproductive effort were body mass and fat levels (Table 3.4). Those variables indicated that physical condition of individuals was the most important factor determining whether individuals became pregnant. Our results are consistent with studies of muskoxen (*Ovibos moschatus*) and caribou (*Rangifer tarandus*) in northern environments where body mass, nutritional condition, and lactational status strongly affected reproduction (Cameron et al. 1993; Gerhart et al. 1997; White et al. 1997). Moreover, maternal fat reserves also are related to body mass in neonatal cervids, with subsequent effects on life-history characteristics, including survivorship (Gaillard et al. 1997; Bowyer et al. 1998; Keech et al. 1999; Barton et al. 2001). Thus, increasing population density, which resulted in lowering of fat reserves and pregnancy in our study also provides a link to survivorship of young (Keech et al. 2000).

We initially were surprised that population density failed ($P > 0.15$) to enter logistic models; however, if effects of population density act through intraspecific competition and decreased physical condition, effects of density were already included in the model (i.e., density was a lurking variable–Framstad et al. 1985, Bowyer et al. 1988).

Failure of population density to enter the logistic model also indicated that socially mediated reduction in reproduction was unlikely, because those measures of condition explained effects of population density on reproduction. If population density had entered the model, that variable likely would indicate that something else related to differing densities (e.g., social stress) was not explained by condition, reproductive effort, and density-independent factors (e.g., precipitation).

Density-dependent factors overrode effects of density-independent factors in this montane ecosystem. Indeed, seasonal temperature, annual precipitation, and seasonal precipitation failed to enter any of our logistic models. Density-independent interactions with density-dependent processes may be more pronounced where effects of density are accumulated through time and where poor physical condition may be aggravated by successive winters resulting in depleted range conditions, a topic in need of additional study.

Elk on Starkey are maintained on a feed ground during winter; thus, effects of different population densities in our study are specific to spring, summer, and autumn. Foraging conditions in winter are controlled by our experimental design. Because elk from both populations were maintained on the same diet throughout winter, we were able to control for effects of winter and focus on differences in nutrition from other seasons, something that is not possible without our experimental approach. Our results indicated strong effects of density dependence on animal condition and pregnancy rates resulting from differences in spring, summer, and autumn nutrition rather than from metabolism of body stores during winter. Because we were specifically testing for effects of density

dependence during summer, we were unable to test those hypotheses relating to carry-over effects of summer or of climatic interactions during winter with population density and age.

Our results support the hypothesis that summer nutrition is critical for building body stores; those animals in the high-density population exhibited lower body condition and reproduction than those at low density. Energy stores are determined by quality of the summer range, while depletion is a function of winter range quality and length of winter (Mautz 1978; Schwartz et al. 1988a, 1988b; Parker et al. 1999). Indeed, animals that are nutritionally stressed and are unable to build adequate body reserves during summer are probably more affected by winter than those animals on a high plane of nutrition during summer (Mautz 1978). We hypothesize that interactions among climate and population density on fecundity and survival are most likely expressed during winter and that young and senescent individuals may be more sensitive to weather severity during winter than prime-aged animals (sensu McCullough 1979).

Our experimental approach to examining density dependence allowed us to compare effects of population density with the same climatic condition for each population density across years. We detected strong density dependence in elk expressed by changes in body condition and reproduction with increasing density. We demonstrated effects of differing nutrition during summer on body condition and reproduction: summer is the most important period for accumulation of body stores to buffer animals against winter. Although summer nutrition was critical for building body stores, severe winters may lead to increased depletion of fat reserves. Consequently, our

results also support the hypothesis that effects of density dependence and measures of K must be viewed as year-round phenomena, rather than during a single season. We suggest that more emphasis be placed on the role of spring and summer on density-dependent processes and thereby population regulation in elk and other northern ungulates.

Acknowledgments

We appreciate the assistance of Starkey Project personnel. R. G. White, M. Vavra, K. J. Hundertmark, J. S. Sedinger, R. W. Ruess, and P. S. Barboza provided helpful comments on the manuscript. E. Rexstad provided valuable expertise in statistical analysis. This study was funded by the United States Forest Service, the Institute of Arctic Biology at the University of Alaska Fairbanks, and the Rob and Bessie Welder Wildlife Foundation. All aspects of this research were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks and the Starkey Project and were in keeping with protocols adopted by the American Society of Mammalogists for field research involving mammals (Animal Care and Use Committee 1998).

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Table 3.1. Life-history characteristics of ungulates and hypotheses tested with this study that reflect the relative differences in a population at low density (at or below maximum sustained yield, MSY) and at high density (at carrying capacity, K), modified from Kie et al. (2003).

LIFE-HISTORY CHARACTERISTIC	POPULATION SIZE AT OR BELOW MSY	POPULATION SIZE AT OR NEAR K	HYPOTHESIS TESTED IN THIS STUDY
Physical condition of adult females	Better	Poorer	Yes
Pregnancy rate of adult females	Higher	Lower	Yes
Age at first reproduction for females	Younger	Older	Yes
Yearlings pregnant	Usually	Seldom	Yes
Pause in annual production by adult females	Less likely	More likely	Yes
Corpora lutea counts of adult females	Higher	Lower	No
Weight of neonates	Heavier	Lighter	No
Litter size[a]	Higher	lower	No

Table 3.1. Continued

LIFE-HISTORY CHARACTERISTIC	POPULATION SIZE AT OR BELOW MSY	POPULATION SIZE AT OR NEAR K	HYPOTHESIS TESTED IN THIS STUDY
Survivorship of young[b]	Higher	Lower	No
Age at extensive tooth wear[c]	Older	Younger	No

[a]No variation in litter size of North American elk.

[b]In the absence of efficient predators

[c]Not applicable because animals did not remain consistently in the same study area.

Table 3.2. Proportions of adult and yearling female elk pregnant and lactating at different population densities during 1998-2001 on the Starkey Experimental Forest and Range, Oregon, USA.

POPULATION CHARACTERISTIC	WEST STUDY AREA		EAST STUDY AREA	
	n	*Proportion*	*n*	*Proportion*
1998				
Population Density (Elk/km^2)		5.41		4.51
Previous Year Pregnancy	4	0.50	7	0.43
Current Year Pregnancy	5	0.20	7	0.43
Lactational Status	5	0.40	7	0.14
1999				
Population Density (Elk/km^2)		6.56		10.79
Previous Year Pregnancy	11	0.64	16	0.44
Current Year Pregnancy	13	0.38	20	0.65
Lactational Status	6	0.33	18	0.22
2000				
Population Density (Elk/km^2)		4.10		20.07
Previous Year Pregnancy	8	0.25	45	0.38
Current Year Pregnancy	8	0.75	46	0.35
Lactational Status	8	0.25	46	0.33

Table 3.2. Continued.

POPULATION CHARACTERISTIC	WEST STUDY AREA		EAST STUDY AREA	
	n	*Proportion*	*n*	*Proportion*
2001				
Population Density (Elk/km^2)		4.10		20.07
Previous Year Pregnancy	15	0.60	34	0.44
Current Year Pregnancy	15	0.53	35	0.37
Lactational Status	15	0.33	33	0.18

Table 3.3. Least-squared means (± *SE*) for body condition indices for adult female elk (*n* = 137) of known age on the Starkey Experimental Forest and Range 1999-2001. Results are from multivariate analysis of covariance with age as covariate; MANCOVA indicated that population density differed for these indices between high and low density populations (*Wilks lambda* $F_{2,133}$= 3.57, P = 0.031).

	Low Density		High Density		
Body Condition Indices	$\bar{X}$	*SE*	$\bar{X}$	*SE*	*P* - value
Rumpfat	0.584	0.030	0.428	0.051	0.009
Body Mass	184.8	3.65	179.7	2.18	0.229

Table 3.4. Results of logistic regression to evaluate pregnancy of adult female elk, n = 138, at the level of the individual from 1998-2001 on the Starkey Experimental Forest and Range, northeastern Oregon, USA. Model evaluation criteria included Hosmer and Lemeshow goodness-of-fit test ($P = 0.043$), Likelihood Ratio Test ($P < 0.001$), AIC = 123.71, with concordance 88.5%.

Variable	DF	Parameter estimate	Standard error	P – value	Odds ratio ψ
Intercept	1	- 13.17	2.566	< 0.001	—
Age	1	- 0.35	0.137	0.011	0.71
Body mass	1	0.07	0.016	< 0.001	1.07
Rumpfat	1	2.55	0.998	0.011	12.82

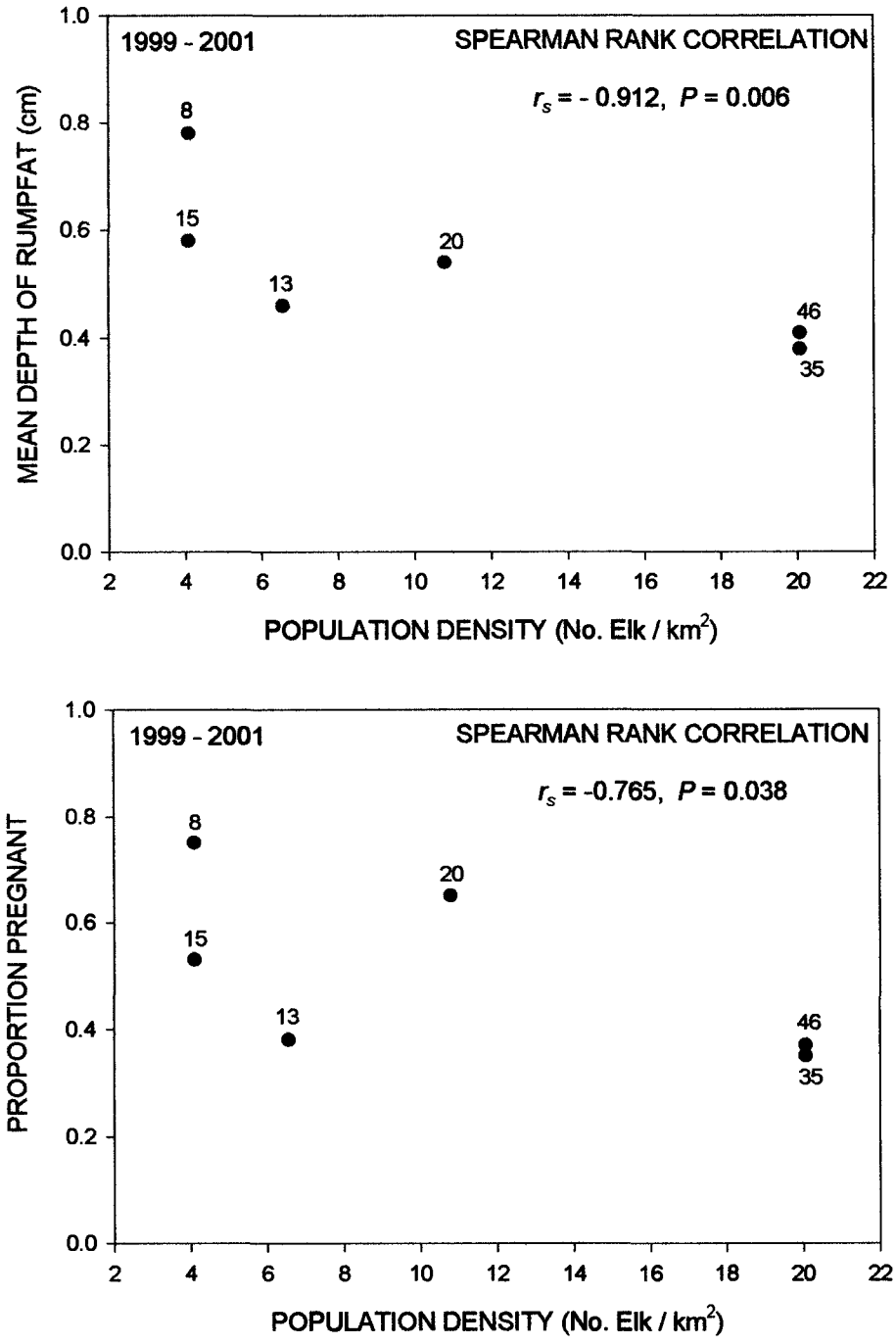

Figure 3.1. Results of one-tailed Spearman Rank Correlations for effects of population density on body condition, indexed by maximal depth of rumpfat (above), and proportion pregnant (below) of yearling and adult female elk combined (n = 137) on the Starkey Experimental Forest and Range, Oregon, USA, 1999-2001.

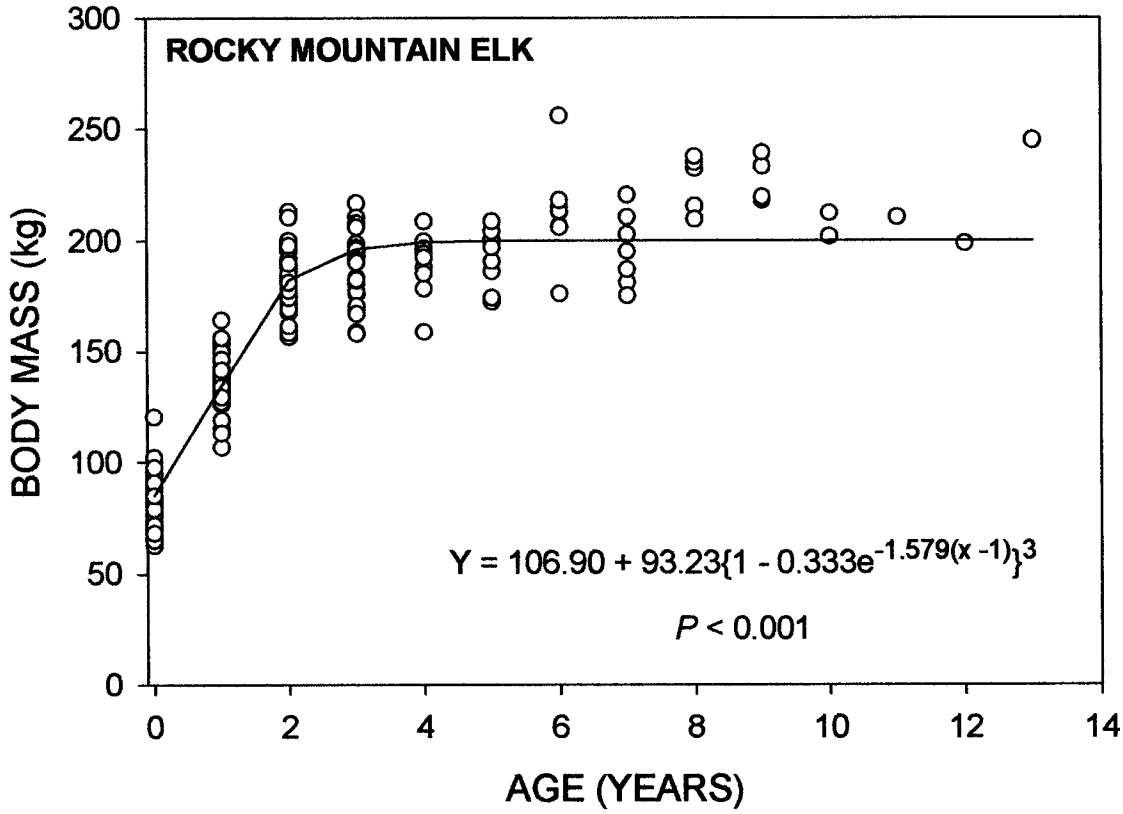

Figure 3.2. Relationship between body mass (kg) and age (years) with the von Bertalanffy equation for sigmoidal growth for 195 female elk on the Starkey Experimental Forest and Range, Oregon USA, 1999-2001. We examined growth curves for both high and low density populations and the resulting curves were identical, thus we used a single curve for all individuals combined.

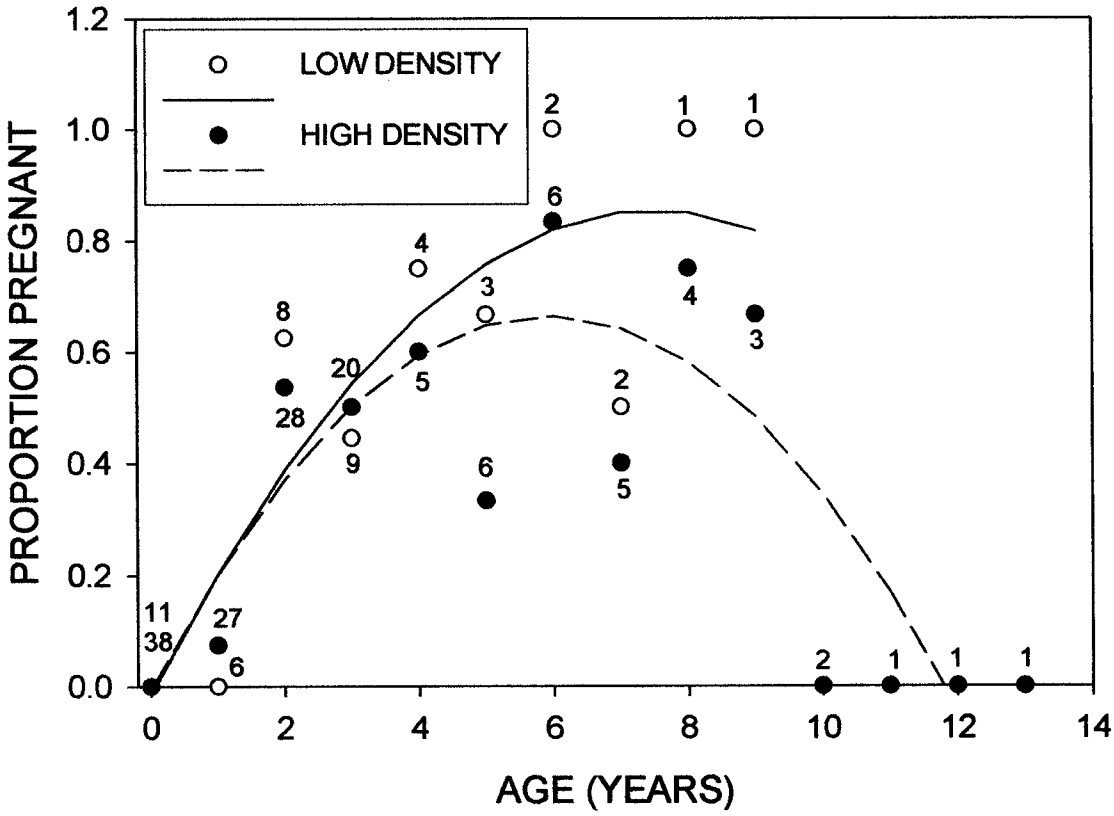

Figure 3.3. Relationships between proportion of female elk pregnant and age for high and low-density areas, weighted by sample size, on the Starkey Experimental Forest and Range, Oregon, USA, 1999-2001. For the high density area (n = 147), the regression was significant ($P < 0.001$, $R^2_{adj} = 0.696$, $\hat{Y} = -0.005 + 0.226\text{Age} - 0.0191\text{Age}^2$. The regression also was significant ($P = 0.005$, $R^2_{adj} = 0.708$, $\hat{Y} = -0.014 + 0.232\text{Age} + 0.016\text{Age}^2$) for the low-density area (n = 47). Sample sizes used in weighted regression analyses are shown next to data points—for the 0 age class 38 young were sampled for the high-density area, and 11 young for the low-density area.

CHAPTER 4[4]

TESTING THE HERBIVORE OPTIMIZATION HYPOTHESIS: EXPERIMENTAL MANIPULATION OF ELK POPULATION DENSITY

Abstract. We designed an experiment to examine interactions related to density of North American elk (*Cervus elaphus*) with plant responses to herbivory in the Blue Mountains of Oregon, USA. We experimentally created high-density and low-density populations of elk and built exclosures to examine effects of herbivory on productivity and species composition of plants. Herbivore optimization is described as the enhancement of net primary production of forage plants with moderate levels of herbivory above that of ungrazed or heavily grazed plants. We hypothesized that if herbivore optimization occurred with increasing population density of elk, a concordant increase in plant production would occur, followed by a decline in productivity as grazing intensity continued to increase. Net aboveground primary productivity (NAPP) increased from no herbivory to moderate grazing intensity and then declined as grazing intensity continued to increase. Apparent offtake followed a similar pattern and was greatest at intermediate levels of grazing intensity, and then declined as NAPP approached zero. We observed no changes in species composition with our density manipulations, probably because of the extensive history of grazing by native and domestic herbivores in the Blue Mountains.

[4] Stewart, K. M., R. T. Bowyer, R. W. Ruess, B. L. Dick, and J. G. Kie. In Prep. Testing the herbivore optimization hypothesis: experimental manipulation of elk population density. Ecology

Our data indicated that increases in NAPP at low to moderate levels of herbivory occurred in montane ecosystems. Compensatory responses by plants are more difficult to detect when responses to herbivory are subtle and occur at relatively low intensity of grazing. We hypothesize that such subtle changes in NAPP from herbivory may be more common than previously thought.

Key words: Cervus elaphus, herbivore optimization, NAPP, North American elk, population density, grazing intensity

INTRODUCTION

The herbivore-optimization model describes the effects of varying levels of grazing pressure on plant production and fitness (Hik and Jefferies 1990). A prediction this model is the enhancement of plant production with moderate levels of herbivory compared with that of ungrazed or heavily grazed plants (McNaughton 1979, 1983, Hilbert et al. 1981, Hik and Jefferies 1990, Bowyer et al. 1997). Herbivores influence or possibly regulate forage quality and availability through changes in plant production, plant species composition, and rates and pathways of nutrient cycling (Coppock et al. 1983, Bazely 1986, Ruess et al. 1989, Hik and Jefferies 1990, Pastor and Naiman 1992, Molvar et al. 1993, van de Koppel et al. 1996, Augustine and Frank 1998, Mulder and Ruess 1998, Frank et al. 2002, Person et al. 2003). Grazing may increase palatability of forages for herbivores by enhancing nitrogen content of above-ground biomass, through shifting demography of plants toward younger and more mitotically active individuals (Bazely and Jefferies 1985, Kotanen and Jefferies 1987). Hik and Jefferies (1990)

reported that intermediate levels of grazing by lesser snow geese (*Chen caerulescens caerulescens*) increased net above-ground primary production (NAPP) on grazing lawns relative to heavily grazed or ungrazed swards. Indeed, Milchunas and Lauenroth (1993) reported that 17% of studies related to grazing showed elevated NAPP in areas grazed compared with areas where grazing was excluded.

Population densities of herbivores and intensity of their foraging may determine whether herbivory increases nutrient cycling and plant productivity (Molvar et al. 1993, Kielland et al. 1997) or negatively affects plant communities by driving changes in successional pathways (Pastor et al. 1997, Jefferies and Rockwell 2002). At high population density, large herbivores exceed their available food resources, thereby initiating density-dependent feedbacks on their physical condition and reproduction (Kie et al. 1983, McCullough 1979, Kie et al. 2003, Stewart et al. In review). There are likely strong interactions among density-dependent processes in large herbivores and effects of their foraging on plant productivity and nutrient cycling, but those interactions have not been studied with an experimental manipulation for large, free-ranging mammals. When herbivores exhibit density-dependent reductions in physical condition and fecundity with increasing population size, a corresponding negative effect on the plant community is expected with reductions in plant productivity and nutrient cycling. Such effects drive changes in successional pathways or lead to degradation of plant communities (Ruess et al. 1998, Jefferies and Rockwell 2002). At sufficiently high densities, large herbivores may denude vegetation (Jefferies and Rockwell 2002) and cause trophic cascades that result in "ecological meltdowns" (Terborgh et al. 2001). Conversely, low or intermediate

levels of herbivory, resulting from populations at low density, initiate positive feedbacks on the plant community with increases in plant production and enhanced nutrient cycling (Hik and Jefferies 1990, Molvar et al. 1993).

Stewart et al. (In review) performed a manipulative experiment to examine effects of density dependence in North American elk (*Cervus elaphus*) by creating free-ranging populations of elk at low (4.1 elk / km^2) and high densities (20.1 elk / km^2). Elk in the low-density population were in better physical condition and had higher rates of reproduction than those in the high-density population (Stewart et al. In review). Concurrent research on density dependence in elk, we studied effects of herbivore population density on NAPP and ecosystem processes. Most studies investing plant responses to herbivory are either clipping experiments (Hjalten et al. 1993, Wardle et al. 2000, Leriche et al. 2003) or examine effects of free-ranging herbivores (du Toit et al. 1990, Hik and Jefferies 1990, Frank and McNaughton 1992, McInnes et al. 1992, Molvar et al. 1993, Augustine and Frank 2001). With this experiment, we were able to manipulate population density on a large scale (1452 ha) and to account for effects of habitat selection on grazing intensity by those large herbivores in our experimental design.

We investigated the interaction between density dependence in a large herbivore and NAPP in the corresponding plant communities at high and low population densities of elk. Accordingly, we tested hypotheses relating to herbivore optimization, and how plant productivity was affected by population densities of elk. We hypothesized that there would be an increase in NAPP initially with increasing population density of elk,

followed by a decline in productivity as grazing intensity continued to increase. Following Hik and Jefferies (1990), we hypothesized that changes in NAPP would be most prevalent during the growing season in spring. We also postulated that rates of vegetation offtake by elk would increase concurrent with increasing productivity, and then decline as grazing intensity continued to increase and NAPP declined. Furthermore, we tested the hypothesis that changes in productivity would result from changes in species composition of plants in the community. Finally, we hypothesized that as productivity increased, we would observe a corresponding increase in rates of N mineralization and soil respiration, resulting from deposition of feces of those large herbivores followed by a corresponding decrease in those rates as grazing intensity continued to increase and productivity declined.

METHODS

Study Area

We conducted research from 1999 through 2001 on the Starkey Experimental Forest and Range (hereafter Starkey) of the U. S. Forest Service. Starkey (45° 12' N, 118° 3' W) is situated in the Blue Mountains of northeastern Oregon and southeastern Washington, USA, and is located 35 km southwest of La Grande, Oregon. Elevations range from 1120 to 1500 m. This site supports a mosaic of forests and grasslands, with moderately sloping uplands dissected by drainages, which are typical summer ranges for elk (Rowland et al. 1997; Johnson et al. 2000). Starkey encompasses 10125 ha, and since 1987 has been surrounded by a 2.4-m fence that prevents immigration or emigration of large herbivores, including migration to traditional winter ranges (Rowland et al. 1997).

We restricted our experiment to the northeast area on Starkey, which encompassed 1452 ha, and was separated from the remainder of the study area by the same high fence (Stewart et al. 2002). The northeast area was divided into 2 study sites, east (842 ha) and west (610 ha), to accommodate experimental comparisons of population densities of elk. We divided the northeast area to ensure that plant communities were in equal proportions in the east and west areas (Stewart et al. 2002; Fig. 4.1.). Study sites of such size are sufficiently large to allow natural movements and other behaviors of large herbivores (McCullough 1979). The high-density population was randomly assigned to the east study area.

Mule deer (*Odocoileus hemionus*) were present in east and west study areas at low population densities. Mean (± SE) population density of mule deer was 3.2 (± 0.71) deer/km^2 in west and 2.1 (± 0.64) deer/km^2 in east study site (Oregon Department of Fish and Wildlife annual helicopter survey 1997-2001). Because this study focused on population density of elk, and deer were present in low densities, no attempt was made to manipulate populations of mule deer.

Seasons were defined by months that grouped within similar ranges of temperature and precipitation, and reflected changes in plant phenology (Stewart et al. 2002). Spring consisted of April through June and exhibited relatively high precipitation (62.1 ± 4.27 mm) and warm (9.1 ± 3.22 °C) temperatures (Stewart et al. 2002). Summer included July through September and had relatively high temperatures (16.0 ± 1.82° C) and low precipitation (22.2 ± 6.16 mm). Autumn was transitional with respect to temperature (7.3 °C) and precipitation (39.5 mm), and included the month of October;

winter ranged from November through March with relatively low temperature (-0.7 ± 2.15 °C) and precipitation (60.5 ± 12.65 mm).

The northeast area consisted of four major plant communities: (1) mesic forest dominated by grand fir (*Abies grandis*); (2) xeric forest characterized by Ponderosa pine (*Pinus ponderosa*); (3) xeric grassland dominated by a few grasses and forbs, including onespike oatgrass (*Danthonia unispicata*), Idaho fescue (*Festuca idahoensis*) and low gumweed (*Grindelia nana*); and (4) logged forest harvested in 1991-1992, and then seeded with grasses including orchardgrass (*Dactylis glomerata*) and bluegrass (*Poa* sp.) and other similar species (Stewart et al. 2002; Fig. 4.1.). Grand fir on Starkey suffered widespread mortality (>90%) from spruce budworm (*Choristoneura occidentalis*) during the late 1980's, and timber was harvested in areas where most trees had been killed (Rowland et al. 1997, Stewart et al. 2002).

Mesic and logged forests had similar soil types, because plant communities were similar prior to harvest (Rowland et al. 1997, Stewart et al. 2002). Those soils were deep with an effective rooting depth ≥150 cm, and well drained; available water capacity was 38-60 cm, consisting primarily of volcanic ash and loess derived from basalt (Dyksterhuis and High 1978). Soils in xeric forests consisted of colluvium and residuum derived from basalt, and were dark reddish-brown and very stony, silty loam (Dyksterhuis and High 1978). Depth to bedrock in xeric forest was 20–50 cm; available water capacity was 2.5–5 cm (Dyksterhuis and High 1978). Grassland soils were similar to those in xeric forests and consisted of colluvium and residuum; soils were shallow and

extremely stony. Production of vegetation was limited by stony substrates, shallow depth to bedrock, and low available water capacity (1 - 2.5 cm; Dyksterhuis and High 1978).

Experimental Design

During 1999, we began an experiment to examine effects of population density of elk on plant productivity and offtake of plant biomass by elk. We compared vegetation responses to herbivory by examining elk populations at high and low densities. We were able to account for habitat selection by elk when examining effects of population density on NAPP because of the ability to manipulate populations of elk on Starkey, use of radio telemetry to determine animal locations, and because exclosures were replicated within habitats and density treatments. Moreover, the size of each of our study areas was at least as large as The George Reserve, where the most extensive research on density dependence of large herbivores was conducted (McCullough 1979).

We selected 4.0 elk/km^2 for the low-density population and 20.0 elk/km^2 for the high-density population based on earlier research conducted on Starkey (Rowland et al. 1997). Our high-density population represented a high concentration of animals; however, nonhunted populations of elk have been reported to attain densities as high as 33 elk/km^2 (Houston 1982; Hobbs et al. 1996, Stewart et al. In review). Hobbs et al. (1996) used 31 elk/km^2 for their high-density treatment in an experiment examining resource competition between cattle (*Bos taurus*) and elk.

Our experiment was begun during May 1999. Within 1 month, however, a gate was left open between study areas, resulting in movement of elk from the high- to the

low-density population (Stewart et al. In review). Thus our low-density population for that year was 6.6 elk/km^2, and the high-density population 10.8 elk/km^2. We maintained a high-density population at 20.1 elk/km^2 and low-density population of 4.1 elk/km^2 for each of the final 2 years of the study.

Elk no longer migrate from the study area to traditional winter ranges because of the fence; those animals were maintained throughout winter in a holding area in which they were fed a maintenance diet of alfalfa hay (Rowland et al. 1997). Elk were trapped and moved onto the winter feedground in early December, via a system of fenced alleys, and were released from that area during late April. Very few elk remain on the study area during winter; consequently herbivory by elk is constrained primarily to spring, summer, and autumn.

During 1998, we placed permanent exclosures in each of the 4 major habitat types, with 3 replications per habitat for each high and low-density treatment. Grassland exclosures were constructed during 1999; thus, data for those areas were not included in calculations for 1999. Exclosures placed in mesic forest, logged forest, and xeric forests were large (32 x 32 m) and totaled 18, whereas exclosures in grasslands were small (12 x 12 m) and totaled 6, to accommodate smaller patches of habitat and lower productivity of those habitats (Fig. 4.1.). Those permanent exclosures in all habitats (24 total) were used in combination with moveable exclusion cages (1 m^2) to estimate seasonal NAPP in the presence and absence of herbivores, and offtake of vegetation by those large mammals. Grazing intensity by elk was determined from animal locations and densities obtained via radio telemetry (Stewart et al. 2002).

Animal Movements and Density

We equipped a subset of animals in each study area with radio transmitters. Because sexual segregation is common among cervids in general (Bowyer 1984, Bowyer et al. 1996, Kie and Bowyer 1999) and for elk in particular (Peek and Lovaas 1968, Weckerly 1998), we equipped both males and females with radio collars. Adult sex ratios often favor females in ungulates (Peterson 1955), and males typically occur at low densities when segregated (Bowyer et al. 1997). Indeed, in each of our study areas we used an adult sex ratio of about 20 adult males to 100 adult females; thus, we equipped 4 males and 8 females with radiocollars in each study area during each year. Locations of radio-collared elk were obtained with a rebroadcast civilian long range navigation (LORAN_C) system from 1999 to 2001 (Findholt et al. 1996). Mean location error of this telemetry system was 52.8 m (SE = 5.87; Findholt et al. 1996). This automated telemetry system located each radiocollared animal approximately every 1.5 h throughout a diel cycle from May to early November each year (Rowland et al. 1997). We restricted our analyses to locations occurring during crepuscular periods for 3 hrs ($\pm$ 1.5 hrs before and after sunrise and sunset), because we were interested in periods when animals were actively foraging. Foraging activity for elk and other ungulates peaks during crepuscular periods (Bowyer 1981, Stewart et al. 2000).

Ungulates do not use their habitats uniformly (Fretwell 1972, Kie et al. 2003); thus, population density for the entire study area was inappropriate for estimating grazing intensity near each exclosure. We estimated density of elk near each exclosure location

using telemetry locations. Data for telemetry locations were determined on a 30 m^2-pixel basis from raster-based GIS maps maintained by the Oregon Department of Fish and Wildlife and the U. S. Forest Service (Rowland et al. 1998). This telemetry system exhibited differences in location rates of animals, which varied spatially across the study area (Johnson et al. 1998). Accordingly each animal location was weighted by the inverse of the correction factor developed for Starkey in each year to mitigate effects of telemetry error in our analyses. We also weighted each animal location by the number of adult females or males that each radio collar represented for each study area and year (Table 4.1). A spatial window of 25 pixels (5 x 5 pixel; 2.25 ha) was used to calculate density of animals (Stewart et al. 2002). We used ArcGIS spatial analyst extension to calculate density of male and female elk for each 2.25 ha spatial window across the entire study area. We used multiresponse permutation procedures (MRPP) to determine if distributions of males and females could be combined or should remain separate (Slauson et al. 1991). Results from MRPP indicated that males and female densities should be calculated separately ($P < 0.0001$); consequently, we created density maps separately for males and females for each year. Those maps were overlaid and summed using ArcGIS spatial analyst, and we smoothed data on density of elk using kriging with spherical models for each year and for spring and summer within years for testing hypotheses specifically related to season (Johnston et al. 2001). Based on those kriged values, we obtained an estimate for population density and thereby an index to grazing intensity at each exclosure location. Our index for grazing intensity was calculated independently from data on NAPP. Population-density estimates around each exclosure were based on

radio-telemetry locations obtained throughout that year or season, and represented a density estimate for that time interval, rather than any specific moment in time.

Vegetation Sampling

We sampled vegetation by clipping using 10, 1-m^2 moveable exclosures in mesic forest, logged forest, and xeric forest and 5 moveable exclosures in grassland habitats. We clipped 0.25-m^2 quadrats inside and outside cages for seasonal productivity of vegetation once per month during spring and summer. Permanent exclosures were sampled using 0.25-m^2 quadrats at the beginning and end of each season to examine NAPP in the absence of herbivory by large mammals. Vegetation was sorted into forage classes: forbs, graminoids, and shrubs. All samples were dried to a constant mass at 45° C to prevent binding of proteins for future nutrient analyses (Robbins 1993) and weighed to the nearest 0.01 g. We estimated NAPP as the difference between biomass within short-term exclosures and unexclosed biomass sampled at the time exclosures were established, divided by interval in days (McNaughton et al. 1996, Person et al. 2003). During 1999, we clipped inside and outside all moveable and permanent exclosures; however, because of limited personnel during 2000 and 2001, we used double sampling of vegetation (Ahmed and Bonham 1982, Bonham 1989) and clipped a subsample of 3 moveable exclosures (inside and out) and 3 quadrats within exclosures, the other 7 moveable exclosures were estimated for biomass of forage categories forbs, graminoids, and shrubs (Ahmed and Bonham 1982, Ahmed et al. 1983, Bonham 1989, Barten et al. 2001). We defined offtake, following Person et al. (1998) as "apparent offtake," because

one of the assumptions of the experiment is that grazing influences the rate of growth of vegetation. Consequently apparent offtake may over or underestimate true offtake, and is also subject to measurement error. We estimated amount of NAPP consumed by summing apparent offtake across periods divided by the interval in days (Person et al. 1998).

During June 2000 and 2001, we quantified species composition of vegetation using step-point transects inside and outside each permanent exclosure (Bowyer and Bleich 1984, Bleich et al. 1997). We recorded a cover "hit" if the point (<1 mm in diameter) fell within the canopy of a shrub or on a stem or leaf of a plant. Points not recorded as cover for plants were litter or bare ground. Each transect contained about 200 step-points outside the exclosure and about 100 step-points inside the exclosure, primarily because of limited space, in a random design. Adequate sample size was determined by plotting the number of species against number of points sampled (Kershaw 1964, Gysel and Lyon 1980, Stewart et al. 2000). We used Morista's Index of Similarity (Krebs 1999) to compare species composition inside and outside each exclosure. We then used linear regression to compare the similarity index to population density (from kriging) to determine if species composition changed outside exclosures with increasing population density. Plant nomenclature follows Hitchcock and Cronquist (1996).

Soil Analyses

We collected 10 soil samples (5 inside and 5 outside each exclosures) with a 10-cm soil corer, during spring 1999 (inside exclosures only), 2000, and 2001. Water

holding capacity (WHC) was measured on a subset of samples collected in 1999 for each soil type represented in the study (Dyksterhuis and High 1978). WHC was defined as the gravimetric water content of sieved soils (2-mm mesh) that were wet to saturation and allowed to drain for approximately 12 h in filter funnels (Paul et al. 1999). Soils were pre-incubated for approximately 11 days to allow microbial populations to stabilize. Soils were analyzed for potential rates of N mineralization and soil respiration. Rates of net nitrogen mineralization were calculated based on performance of 12 g soil placed in separate 150 ml specimen cups. Each pair of cups was placed in a 1-l mason jar in an incubator, and held in aerobic microcosms at 60% WHC and 22° C over 20 days (Robertson et al. 1999). Nitrogen was extracted with K_2SO_4 under a vacuum. Solution NH_4^+-N and NO_2/NO_3-N were then analyzed colorimetrically on a modified Technicon autoanalyzer (Tarrytown, New York, USA). Net N mineralization potentials were calculated as the difference in extractable N (NH_4–N + NO_3–N) between the end and beginning of the incubation period (Molvar et al. 1993, Robertson et al. 1999). Negative values for N mineralization were included in calculation of means for each exclosure site. Net C mineralization potentials were determined by dividing the headspace CO_2 concentration by the duration of the incubation. We assumed that the initial headspace CO_2 concentration at T_0 was at 500 ppm, and this value was subtracted from the calculations (Robertson et al. 1999).

Statistical Analyses

We used regression to compare vegetation and soil data with intensity of grazing (e.g., population density) by elk. Data on vegetation included annual NAPP, rate of vegetation offtake by herbivores, Morista's Similarity Index (exclosure with outside). Data on soils included potential rates of soil respiration and N mineralization. We used multivariate analysis of variance (MANOVA) to compare our index of similarity (inside to outside exclosures at each site) to the high- and low-population density treatments.

Because of the highly variable nature of plant communities (Barten et al. 2001, Lenart et al. 2002), we designed our experiment to cover a range of habitats with large number of replications, so that effects of treatments could be detected. Because of the patchy nature of habitats across the study areas (Fig. 4.1), we had to account for habitat selection in addition to forage selection by elk. Moreover, because of the automated telemetry system, we were able to assess grazing intensity of herbivores at each exclosure site across both study areas to obtain a wide range of population densities to gain a better understanding of the effects of densities of herbivores on plant communities.

RESULTS

We tested for differences in habitats for NAPP to determine if habitats should be combined or should remain separated. Significant differences in NAPP occurred among habitats ($P < 0.001$), and for a habitat by population density interaction ($P < 0.001$, Fig. 4.2). Mesic and logged forests differed from xeric forests and grasslands in NAPP; we observed the same pattern when we examined functional groups of plants separately (Fig.

4.2). Thus, we combined mesic and logged forest habitats, classed as high NAPP habitats, and xeric forest and grasslands were combined and classed as low NAPP habitats because of lower NAPP (Fig. 4.2). High and low NAPP habitats were examined separately in all further analyses.

We used kriging to model population density of elk across the entire northeast study area for each year (Fig. 4.3). From those kriged values, we obtained both annual and seasonal estimates of population density that were specific to the area immediately surrounding each exclosure. We observed a curvilinear relationship between NAPP and population density of elk for high NAPP habitats, with NAPP increasing at low levels of herbivory and decreasing as population density of elk increased (Table 4.2). This relationship was consistent when we examined those regressions for each plant functional group, although that relationship was not significant for shrubs (Table 4.2). Conversely, those relationships did not hold in low NAPP habitats, however. Regression of NAPP and population density was not significant for all plant categories combined (Table 4.2). When we examined seasonal effects of herbivory on NAPP, we observed significant effects of elk density on NAPP during spring in high NAPP habitats, for all functional groups of plants combined (Fig. 4.4); those relationships were not significant in low NAPP habitats (Table 4.2). During spring we observed curvilinear relationship for forbs, graminoids and shrubs in high-NAPP habitats (Fig 4.4). Those effects were not present during summer in high or low-NAPP habitats (Table 4.2). We also observed a similar relationship between rate of offtake of vegetation by herbivores and population density of elk, in which rate of offtake increased at low population densities and then decreased as

population density increased for both high and low-NAPP habitats (Fig. 4.5). Those relationships were similar for functional groups in high-NAPP habitats (Fig 4.6) and for graminoids in low-NAPP habitats (Fig. 4.6). There was not a significant curvilinear relationship between offtake and population density for forbs ($R_a^2 < 0.001$, $P = 0.442$) or shrubs ($R_a^2 < 0.001$, $P = 0.658$). We observed no significant relationships ($R^2 = 0.048$, $P = 0.124$) from linear regression between Morista's Index of similarity inside versus outside exclosures and population density of elk, indicating little change in species composition of plants with herbivore density (Appendix 4A).

We estimated soil respiration and N mineralization for exclosures, low and high-density treatments in high and low-NAPP habitats (Table 4.3). We observed no relationship between population density of elk and potential rates of soil respiration ($R^2 = -0.016$, $P = 0.952$) for all habitats or when habitats were combined into high ($R_a^2 = -0.032$, $P = 0.952$) or low ($R_a^2 = -0.029$, $P = 0.833$) NAPP. N mineralization likewise had no relationship with population density ($R_a^2 = 0.004$, $P = 0.294$) for all habitats combined or for those in high- ($R_a^2 = -0.017$, $P = 0.585$) or low- ($R_a^2 = 0.018$, $P = 0.224$) NAPP habitats.

DISCUSSION

Net above-ground primary production (NAPP) increased at low to intermediate levels of herbivory and then declined at higher levels of herbivory, which supported predictions of the herbivore optimization hypothesis. Those relationships were strong in high-NAPP habitats, but were not apparent in less-productive ones (Table 4.2).

Curvilinear relationships between NAPP and population density were evident during spring and for all functional groups of plants, but were not manifested during summer (Fig. 4.4). This result likely occurred because of the lower water availability during summer when plants in this montane ecosystem were no longer growing (Stewart et al. 2002). Moreover, our analysis of NAPP on an annual basis (Table 4.2) likely was driven by those processes that occurred during spring, when most growth of plants occurred (Fig. 4.4).

We observed a curvilinear relationship between apparent rate of vegetation offtake and population density of elk, in which offtake increased at low levels of herbivory and then declined with increasing population density (Fig. 4.5). This relationship was consistent in both high and low NAPP habitats. Indeed, when we examined functional groups of plants separately, forbs, graminoids, and shrubs showed curvilinear relationships in offtake with population density in high-NAPP habitats (Fig 4.6). Conversely, in low-NAPP habitats, only graminoids showed a curvilinear relationship with population density likely indicating that the relationship in low NAPP habitats was driven by changes in graminoids rather than by use of other functional groups. In addition, low-NAPP habitats were typically dominated annual and perennial grasses, although very early in spring those habitats contained many annual forbs. Even in high-NAPP habitats, graminoids showed the strongest effects of offtake as influenced by population density (Fig. 4.6). Annual NAPP and apparent offtake peaked at similar levels of grazing intensity: NAPP = 18 elk/ km^2, and apparent offtake = 23 elk / km^2. NAPP was zero at about 42 elk / km^2—that observation was concordent with apparent

offtake, which was zero at about 43 elk / km^2. At low levels of herbivory, removal of vegetation by herbivores increased with increasing NAPP. Conversely, at high population densities, offtake declined as forage availability declined because less forage was available for removal even though more elk were present. In addition, elk may have removed more than current annual growth of shrubs and some graminoids in those high-NAPP habitats.

Some values of NAPP in both habitat classes were negative, although primarily in low-NAPP habitats (Fig 4.2). Those negative values likely occurred because of changes in plant phenology within functional groups. Phenology changed rapidly in low-NAPP habitats. During the initial sampling period in spring, those habitats were dominated by annual forbs; the next sampling period the vegetation had shifted to primarily annual grasses, although a few perennial grasses and forbs were present. The final sampling period during spring contained vegetation in late phenological stages, in essence standing dead material, although a few perennial forbs and grasses remained viable. Thus, calculations for NAPP likely resulted in negative values for those functional groups in low-NAPP habitats. To improve estimates of NAPP in low-NAPP habitats the frequency of sampling should likely be much higher to improve precision and accuracy in estimates of NAPP. Furthermore, more frequent sampling of vegetation in those habitats may improve our ability to detect possible increases in NAPP with herbivory, although likely at much lower levels than we observed in high-NAPP habitats. We hypothesize that optimization may occur in those habitats, but at small perturbations that we were unable to detect.

Changes in NAPP that we observed were not likely a result of differences in species composition of the plant community; we failed to observe changes in Morista's Index of Similarity between density treatments. The Blue Mountains in eastern Oregon have an extensive history of grazing by high-density populations of native and domestic herbivores (Skovlin 1991). Fuhlendorf et al. (2001) reported that herbivory established long-term directions of plant composition and structure and that, over time, grazing exerted a continuous selective influence on individual plant species or functional groups. Thus, this area likely is resistent to changes in species composition from herbivory; most plant species present in this system probably are relatively grazing tolerant. We hypothesize that maintenance of this experiment through time would lead to increased prevalence of grazing-sensitive species in the low-density area, provided that root stock or seed banks have remained viable in the soil. We note, however, that we obtained evidence of herbivore optimization in a relatively short time, indicating the importance of large herbivores in affecting ecosystem processes.

Probably the best examples of increasing NAPP and herbivore optimization with intermediate levels of herbivory occur in ecosystems that support high densities of herbivores such as grasslands in Africa and North America (Detling 1988, Huntly 1991, Frank and McNaughton 1993, Frank et al. 1998) or sub-arctic salt marshes (Hik and Jefferies 1990), where graminoids are often modified to prostrate, rapidly growing forms that are more nutritious and resilient to herbivory (McNaughton 1979, 1983, Hik and Jefferies 1990, Person et al. 2003). In those ecosystems that support large numbers of herbivores, increases in NAPP do not appear to occur without deposition of urine and

feces that increase cycling of nutrients, particularly N (Hik and Jeffereis 1990, Ruess and McNaughton 1988, Grank and Groffman 1998, Augustine and Frank 2001). This stimulation of NAPP does not appear to be restricted to graminoid-dominated systems, however. African browsers stimulated shoot production and enhanced browse quality of *Acacia* species near watering holes (du Toit et al. 1990), and moose (*Alces alces*) in interior Alaska increased rates of N cycling and NAPP of willow- (*Salix* sp.) dominated systems (Molvar et al. 1993). Similarly, our data also indicate increased NAPP in forbs and shrubs as well as graminoids. Those increases in NAPP in response to intermediate levels of foraging occurred at lower levels of herbivory than exhibited in ecosystems dominated by graminoids. Most populations of moose in interior Alaska are held at relatively low population density by predation (Gasaway et al. 1992, Bowyer et al. 1998), which likely prevents heavy browsing and allows for positive feedbacks in stimulating production of willows and cycling of N (Molvar et al. 1993). Those increases in NAPP that we observed on Starkey occurred at low to moderate levels of grazing intensity without the change in growth forms of plants that have been observed in Arctic and African ecosystems dominated by graminoids (Hik and Jefferies 1990, McNaughton 1979, 1983). This difference among systems probably occurred because stimulation of NAPP in response to herbivory occurred at much lower levels of grazing intensity on Starkey. Moreover, stimulation of NAPP on Starkey may not necessarily have resulted from inputs of urine and feces following herbivory by elk because we observed no differences in N mineralization across a range of intensities of grazing. Changes in N cycling, however, may have occurred in small, localized patches that we were unable to

detect. Augustine and Frank (2001) noted very fine-grained variability in soil N and N-mineralization potential in grazed grasslands compared with ungrazed areas that exhibited no spatial structure in soil N properties.

Herbivore optimization may occur in numerous systems, although probably at low population densities of herbivores and with small increases in NAPP that are easily overlooked. Milchunas and Lauenroth (1993) reported that 17% of studies showed elevated NAPP in areas grazed relative ungrazed areas. Many of the studies reviewed by Milchunas and Lauenroth (1993), however, examined effects of domestic herbivores—livestock grazing tends to be more intense and spatially constant than grazing by native herbivores (Hobbs 1996). Increases in NAPP are predicted to occur at moderate levels of herbivory and studies of herbivory from domestic herbivores may underestimate the prevalence of compensatory responses by plants (Hobbs 1996). The wide range of grazing intensities that we observed allowed us to detect those relatively subtle changes in NAPP in response to herbivory by large herbivores. Although we report high-population densities of elk across our exclosure sites, our densities reflect the cumulative density of elk over a season (e.g., spring or summer) or time interval (May – September), rather than that number of animals on any given site for an extended period of time. Nevertheless, stimulation of NAPP occurred at low to moderate levels of herbivory and declined as grazing intensity increased.

Decreases in NAPP that we observed at high population densities correspond with density-dependent reductions in physical condition and reproduction of female elk in the high-density treatment (Stewart et al. In review). As population density increased and

NAPP was reduced, herbivores were forced to use lower-quality forage as those younger, actively growing shoots became unavailable. Conversely, in our low-density treatment, NAPP was greater than inside permanent exclosures, elk were in better physical condition and exhibited enhanced reproduction. Thus, effects of herbivory on NAPP are strongly associated with density-dependent processes in populations of herbivores.

At high population densities, herbivores have the capacity to alter successional patterns and change structure of plant communities to those dominated by unpalatable species (McInnes et al. 1992, Pastor et al. 1993, Pastor and Cohen 1997) or lead to degradation of soils and loss of vegetation in plant communities (Jefferies and Rockwell 2002). Such changes in successional patterns may lower ecological carrying capacity (*K*), so that those habitats support lower numbers of herbivores (McCullough 1979). Conversely at intermediate levels of herbivory, herbivores may improve quality and quantity of available forage. Person et al. (2003) reported increases in mass of juvenile black brant (*Branta bernicla nigricans*) with increases in surface area of grazing lawns in southwestern Alaska, where continued foraging by those birds led to increases in distribution of grazing lawns. That population had previously been exhibiting negative feedbacks associated with density-dependent reduction in mass of juveniles. Thus, a positive feedback resulted between grazing by black brant leading to increased area of grazing lawns and increased gosling mass (Person et al. 2003).

In most ecosystems, high levels of herbivory lead to declines in NAPP (McNaughton 1979, 1983). Compensatory responses by plants are more difficult to detect when responses to herbivory are more subtle and occur at relatively low to

moderate intensities of grazing. Large herbivores do not use habitats uniformly (Fretwell 1972, Hobbs 1996); our experimental design allowed us to account for habitat selection by those large herbivores, while simultaneously examining the effects of grazing intensity on forage classes within habitats. This experimental approach, combined with an independent measure of grazing intensity to directly evaluate presence of elk, permitted us to detect those subtle changes in NAPP within habitats in response to varying levels of herbivory. Moreover, coupling changes in NAPP, species composition, and nutrient cycling in response to herbivory with density-dependent processes allows us to better understand and conserve ecosystems with populations of large herbivores.

ACKNOWLEDGMENTS

We appreciate the assistance of Starkey Project personnel, especially those involved with collection of field data and building exclosures R. Kennedy, R. J. Stussy, J. Nothwang, P. Kennington, L Naylor, A. Stokes, J. Anderson and T. W. Heater. Numerous volunteers and seasonal employees also aided in data collection. E. Rexstad provided valuable statistical assistance and C. P. H. Mulder provided helpful information on Similarity Indices. K. Keilland provided lab space and supplies for soil analyses. B. T. Person, D. K. Person, J. S. Sedinger, and M. Vavra provided helpful comments on the manuscript. This study was funded by the U. S. Forest Service, the Institute of Arctic Biology at the University of Alaska Fairbanks, and the Rob and Bessie Welder Wildlife Foundation. All aspects of this research were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks and the Starkey Project and

were in keeping with protocols adopted by the American Society of Mammalogists for field research involving mammals (Animal Care and Use Committee 1998).

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Table 4.1. Correction factors for number of adult female and male elk at each radio telemetry location used to calculate population density of elk in 2.25-ha spatial window on Starkey Experimental Forest, northeastern Oregon, 1999-2001.

	1999				2000				2001			
	West Study Area		East Study Area		West Study Area		East Study Area		West Study Area		East Study Area	
Variable	Adult Males	Adult Females	Adult Males	Adult Females	Adult Males	Adult Females	Adult Males	Adult Females	Adult Males	Adult Females	Adult Males	Adult Females
Population Density (Elk / km^2)	6.56		10.79		4.10		20.07		4.01		20.07	
No. Elk	5	22	11	63	5	16	17	105	5	17	20	116
No. Radio Collars	4	8	4	8	4	8	4	8	4	8	4	8
Correction Factor (No. Elk / Collar)	1	3	1	8	1	2	5	14	1	3	5	15

Table 4.2. Results of regressions to examine annual and seasonal NAPP ($\hat{Y}$) versus population density (x) of elk on the Starkey Experimental Forest and Range, Oregon, USA, 1999-2001. Habitats were divided into high NAPP (mesic and logged forest) and low NAPP (xeric forest and grasslands) based on significant ANOVA ($P < 0.001$). Note: results for spring, high NAPP habitats are shown in figure 3

NAPP	EQUATION	R_a^2	P-value
Annual			
High NAPP Habitats	$\hat{Y} = 1.79 + 0.14x - 0.003x^2$	0.143	0.002
Forbs	$\hat{Y} = 0.26 + 0.03x - 0.002x^2$	0.100	0.010
Graminoids	$\hat{Y} = 0.35 + 0.09x - 0.002x^2$	0.174	> 0.001
Shrubs	$\hat{Y} = 0.58 + 0.02x - 0.0004x^2$	0.013	0.647
Low NAPP Habitats	$\hat{Y} = -0.13 + 0.04x - 0.002x^2$	0.037	0.115
Spring			
Low NAPP Habitats	$\hat{Y} = 0.116 + 0.083x - 0.005x^2$	0.032	0.134
Summer			
High NAPP Habitats	$\hat{Y} = -0.076 - 0.152s + 0.007x^2$	0.034	0.112
Low NAPP Habitats	$\hat{Y} = -0.313 - 0.019x + 0.001x^2$	- 0.027	0.865

Table 4.3. Descriptive statistics for soil data and treatments of no herbivory (inside exclosures), low-density treatment (west study area), and high-density treatment (east study area) by habitats of high (mesic and logged forest) and low (xeric forest and grasslands) NAPP on the Starkey Experimental Forest and Range, Oregon, USA, 1999-2001.

	Population Density								
	No Herbivory			Low Density (4.1 elk / km^2)			High Density (20.1 elk / km^2)		
Soil Variables	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE
High NAPP Habitats									
Soil Respiration (CO_2 μmol / g soil / day)	24	1.12	0.113	18	1.32	0.068	18	1.12	0.146
N Mineralization (N mg / kg soil /day)	23	0.23	0.494	15	0.15	0.069	18	0.28	0.057
Low NAPP Habitats									
Soil Respiration (CO_2 μmol / g soil / day)	24	1.19	0.133	18	1.09	0.127	18	1.14	0.150
N Mineralization (N mg / kg soil /day)	24	0.29	0.080	18	0.15	0.085	17	0.13	0.055

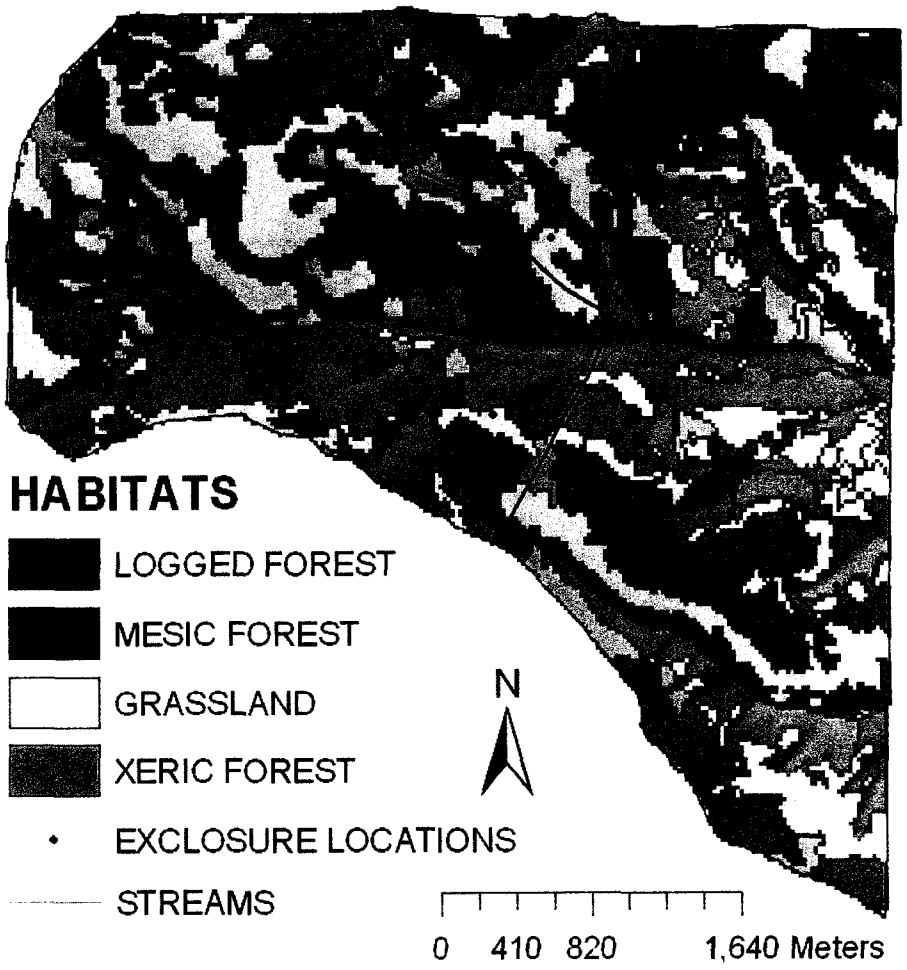

Figure. 4.1. Map of northeast study area with east and west areas for manipulation of population density of North American elk on the Starkey Experimental Forest and Range, Oregon, USA. Four major habitat types are indicated with corresponding locations of herbivore exclosures.

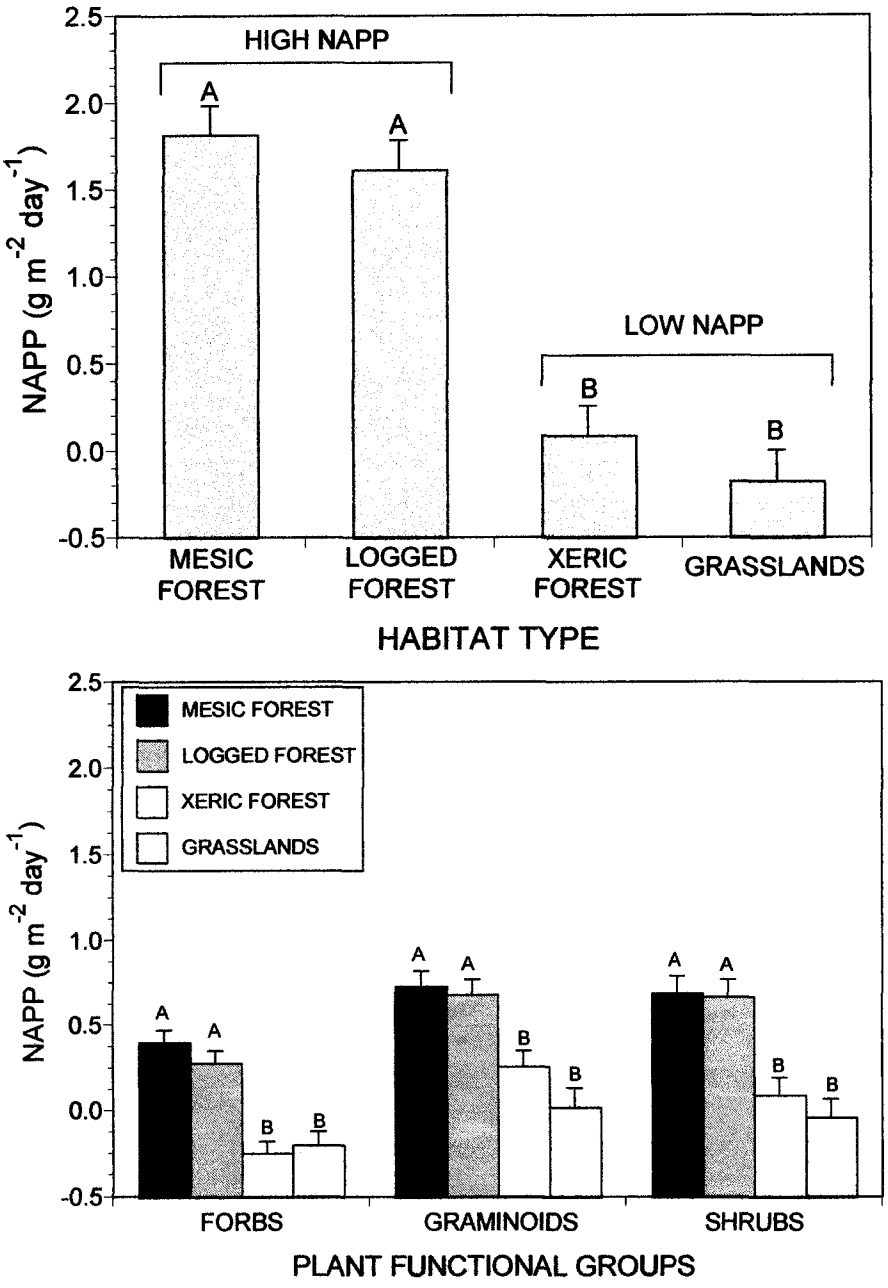

Fig. 4.2. A. Mean (± SE) net aboveground primary productivity (NAPP) for 4 major habitat types in the northeastern study area on the Starkey Experimental Forest and Range, Oregon, USA, (1999-2001). Letters over bars indicate results of comparisons following significant ANOVA ($F_{3, 124} = 36.62$, $P < 0.001$), in which different letters indicate significant differences ($P < 0.001$). B. Mean (+ SE) of NAPP for each functional group of plants among 4 habitat types on the Starkey Experimental Forest and Range. Letters over bars indicate results of comparisons following significant MANOVA (*Wilks lambda* $F_{9, 273} = 11.88$, $P < 0.001$).

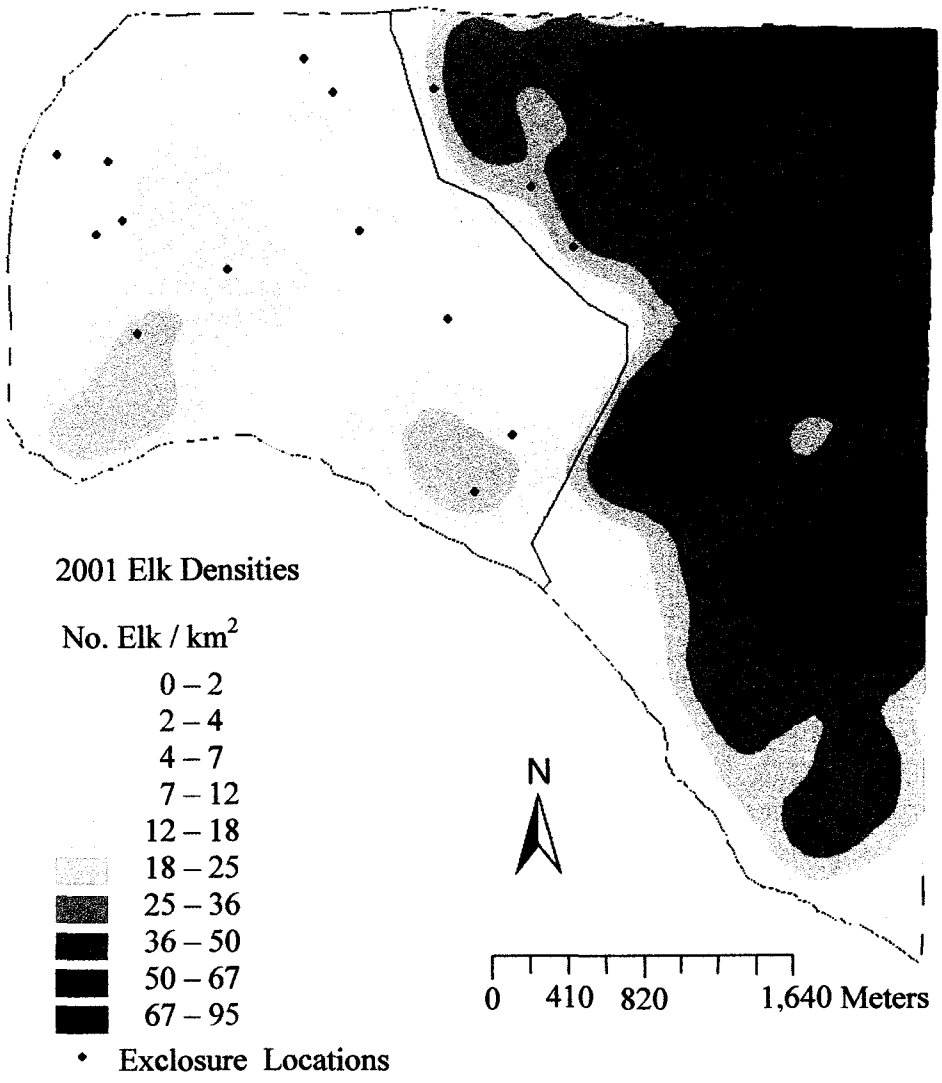

Figure. 4.3. Example of kriged contours indicating cumulative elk population density over 2001 spring and summer seasons (May – September) on the Starkey Experimental Forest and Range, Oregon, USA.

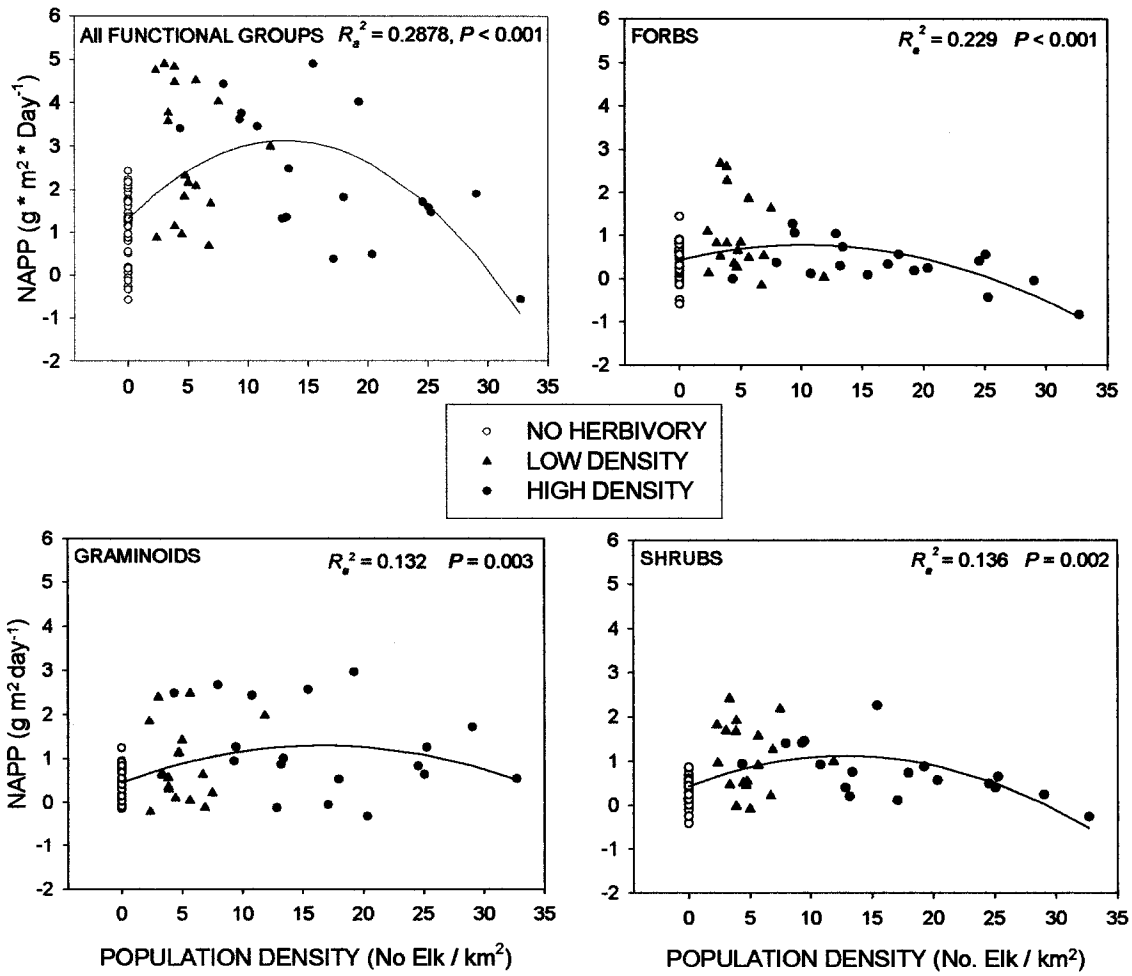

Fig. 4.4. Results of regression analysis examining NAPP versus cumulative population density of elk for spring season (May – June) as estimated from kriged densities across east and west study areas on the Starkey Experimental Forest and Range, Oregon, USA, 1999-2001. Habitats were divided into high NAPP (mesic and logged forest) and low NAPP (xeric forest and grasslands) based on significant ANOVA ($P < 0.001$). No herbivory occurred inside permanent exclosures, low density treatment was west study area and high density treatment was east study area. Regressions were significant for all functional groups ($\hat{Y} = 1.32 + 0.28x - 0.01x^2$), forbs ($\hat{Y} = 0.43 + 0.11x - 0.004x^2$), graminoids ($\hat{Y} = 0.46 + 0.10x - 0.003x^2$), and shrubs ($\hat{Y} = 0.43 + 0.07x - 0.003x^2$).

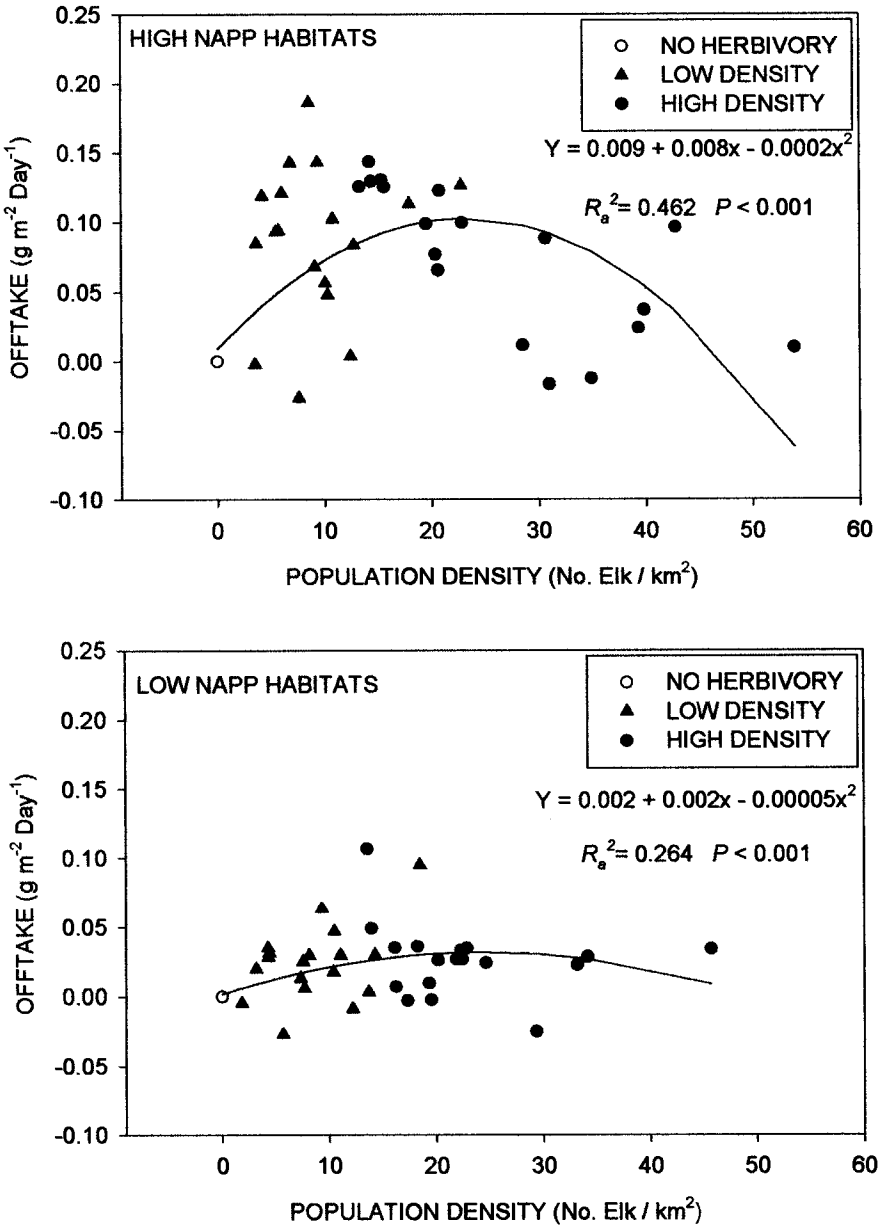

Fig. 4.5. Results of regression analysis examining rates of apparent offtake versus cumulative population density of elk (May – September) as estimated from kriged densities across east and west study areas on the Starkey Experimental Forest and Range, Oregon, USA, 1999-2001. Habitats were divided into High NAPP (mesic and logged forest) and low NAPP (xeric forest and grasslands) based on significant ANOVA ($P < 0.001$). No herbivory is measured inside exclosures, the low-density treatment was the west study area (4.1 elk km^{-2}) and high-density treatment was east study area (20.1 elk km^{-2}). Note: point representing 0 apparent offtake by large herbivores represents 36 samples each for good and poor quality habitats.

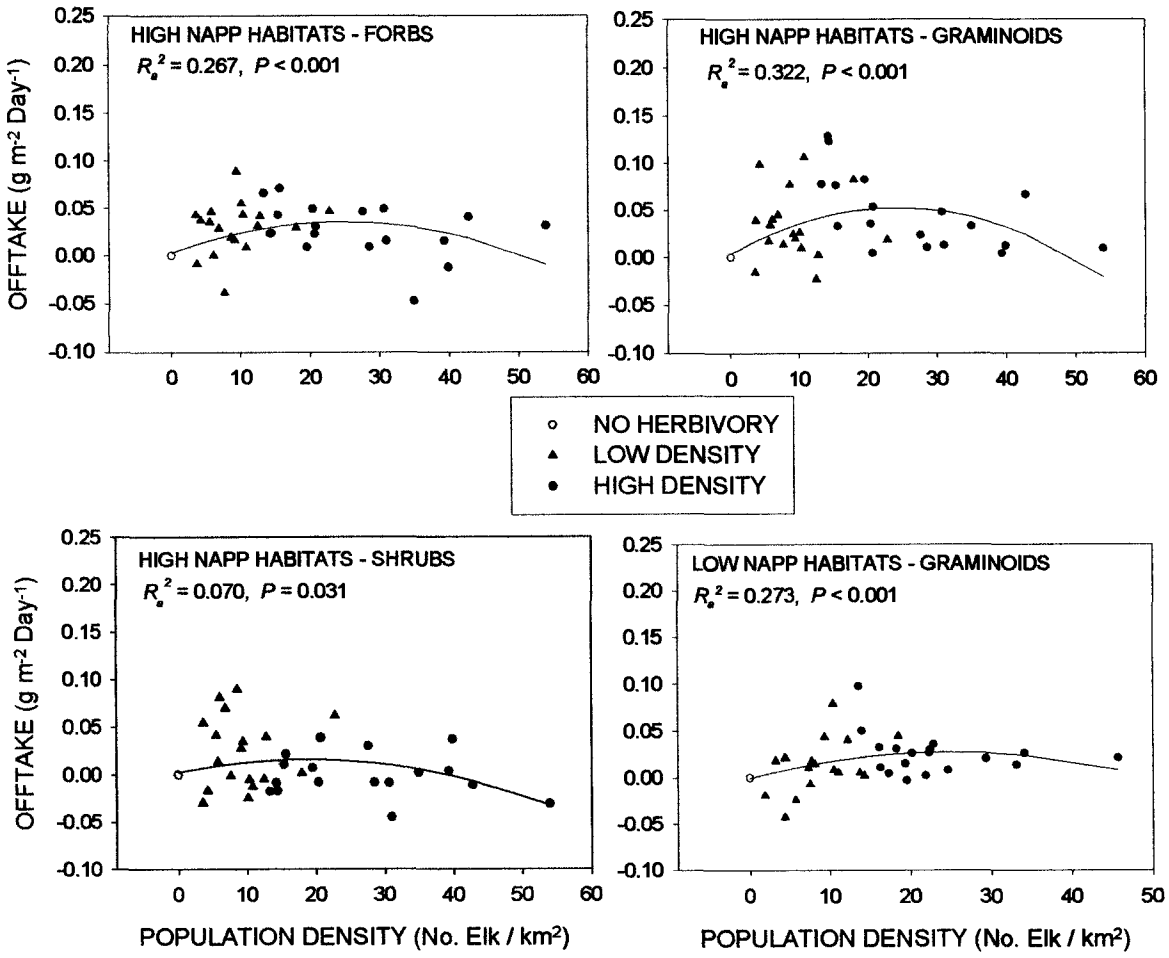

Fig. 4.6. Results of regression analysis examining rates of apparent offtake by functional groups of plants versus cumulative population density of elk (May-September) as estimated from kriged densities across east and west study areas on the Starkey Experimental Forest and Range, Oregon, USA, 1999-2001. Habitats were divided into high NAPP (mesic and logged forest) and low NAPP (xeric forest and grasslands) based on significant ANOVA ($P < 0.001$). No herbivory is measured inside herbivory exclosures, low density treatment was west study area (4.1 elk km^{-2}) and high density treatment was east study area (20.1 elk km^{-2}). Regression were significant for forbs ($\hat{Y} = 0.003 + 0.002x - 0.00005x^2$), graminoids ($\hat{Y} = 0.004 + 0.004x - 0.00008x^2$) and shrubs ($\hat{Y} = 0.003 + 0.001 - 0.00004x^2$) in high NAPP habitats, and for graminoids ($\hat{Y} = -0.0003 + 0.002x - 0.00004x^2$) in low NAPP habitats. Note: point representing 0 apparent offtake by large herbivores represents 36 samples each for high and low NAPP habitats.

APPENDIX 4A

Table 4A. Mean (± SD) number of individuals of plant species used in calculations for Morista's Index of Similarity on the Starkey Experimental Forest and Range 2000-2001.

	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
SPECIES	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
MESIC FOREST						
Achillea millefolium	0.6	0.52	1.7	1.37	1.0	0.00
Adenocaulon bicolor	0.3	0.50	0.5	0.71	0.5	0.71
Amelanchier alnifolia	1.3	1.58	0.3	0.52	2.5	0.71
Anaphalis margaritacea	0.5	0.71	0.0	0.00	0.0	0.00
Antennaria luzuloides	0.5	1.00	0.5	0.71	0.5	0.71
Antennaria rosea	0.3	0.50	0.3	0.50	0.0	0.00
Aquilegia formosa	1.1	1.60	0.3	0.50	0.8	0.75
Arnica cordifolia	4.2	2.52	4.8	5.27	5.7	4.84
Arnica sororia	0.0	0.00	0.5	0.58	0.0	0.00
Arenaria macrophylla	0.5	0.55	0.0	0.00	0.5	0.58
Arctostaphylos uva-ursi	1.7	1.83	3.8	1.17	1.8	1.83
Aster conspicuus	1.0	1.41	0.3	0.50	0.3	0.50
Astragalus sp.	0.7	0.82	2.0	1.41	0.3	0.50
Berberis repens	0.5	0.67	2.0	0.89	1.0	2.00
Bromus carinatus / inermis	0.8	1.04	0.0	0.00	0.3	0.50
Bromus tectorum	0.0	0.00	0.5	0.71	0.0	0.00
Carex geyeri	3.7	1.97	8.2	3.12	9.2	6.55
Calochortus sp.	0.5	0.53	0.5	1.00	0.5	1.00

Appendix 4.A Continued.

SPECIES	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Carex rossii / concinnoides	0.4	0.75	0.5	0.71	1.3	1.86
Calamagrostis rubescens	5.7	3.85	11.5	4.97	12.0	5.66
Chimaphila umbellata	1.3	1.16	2.7	3.27	3.3	2.87
Cirsium vulgare	0.3	0.50	0.0	0.00	0.5	0.71
Collomia sp.	0.5	0.71	0.0	0.00	0.0	0.00
Collinsia parviflora	0.0	0.00	0.0	0.00	0.5	0.71
Cypripedium montanum	0.0	0.00	0.0	0.00	0.5	0.71
Dactylis glomerata	0.5	0.58	0.0	0.00	0.5	0.71
Disporum trachycarpum	0.8	0.89	0.0	0.00	1.2	1.60
Dodecatheon sp.	0.0	0.00	0.5	0.71	0.0	0.00
Elymus glaucus	0.3	0.50	0.5	0.71	0.0	0.00
Epilobium angustifolium	0.9	1.29	1.0	1.55	1.8	1.71
Epilobium paniculatum	0.0	0.00	0.5	0.71	0.0	0.00
Epilobium watsonii	0.0	0.00	0.0	0.00	0.5	0.71
Festuca occidentalis	0.7	0.67	0.7	0.82	0.5	0.58
Frasera speciosa	0.3	0.50	1.0	1.41	0.0	0.00
Fritillaria pudica	0.0	0.00	0.0	0.00	1.5	2.12
Fragaria vesca	2.3	1.91	3.2	2.40	6.7	3.78
Fragaria virginiana	0.8	0.75	2.2	1.60	1.2	1.47
Galium triflorum	1.7	1.97	1.0	1.55	2.5	1.64
Geranium viscosissimum	0.5	0.71	0.0	0.00	0.0	0.00

Appendix 4A Continued.

SPECIES	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Hieracium albiflorum	1.5	1.31	1.0	0.63	1.0	1.41
Hieracium albertinum	1.4	1.07	2.7	3.67	0.5	0.58
Holodicsus discolor	1.0	1.41	0.0	0.00	0.0	0.00
Linnaea borealis	3.2	2.33	4.8	5.08	8.7	2.80
Lonicera involucrata	0.5	0.84	0.5	0.71	0.5	1.00
Lupinus caudatus	4.7	4.57	4.0	4.32	3.3	3.08
Lupinus sericeus	0.3	0.50	1.5	0.71	0.5	0.71
Luzula campestris	0.5	0.71	0.0	0.00	1.0	1.41
Madia gracilis	0.0	0.00	0.5	0.71	0.0	0.00
Microseris nutans	0.0	0.00	0.5	0.71	0.0	0.00
Microseris troximoides	0.8	0.96	0.0	0.00	0.5	0.71
Microsteris gracilis	0.3	0.50	0.0	0.00	0.0	0.00
Mitella stauropetala	0.7	0.92	2.0	2.82	1.3	2.80
Osmorhiza chilensis	0.9	1.29	1.3	1.26	2.0	1.10
Pachistima myrsinites	5.0	0.00	2.5	2.12	0.0	0.00
Penstemon confertus	0.5	0.71	0.0	0.00	0.0	0.00
Penstemon deustus	0.5	0.71	0.0	0.00	0.0	0.00
Potentilla glandulosa	0.6	0.74	0.5	0.58	0.0	0.00
Potentilla gracilis	0.3	0.50	0.0	0.00	0.5	0.71
Prunella vulgaris	0.5	0.71	0.0	0.00	0.0	0.00
Pyrola secunda	0.3	0.67	1.0	0.82	1.5	1.87

Appendix 4A Continued.

SPECIES	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Ranunculus sp.	0.6	0.92	1.0	1.41	0.5	1.00
Ribes sp.	1.3	1.37	0.5	0.71	0.75	0.96
Rosa sp.	2.3	2.27	2.3	2.34	2.8	2.48
Rumex occidentalis	0.0	0.00	1.0	0.82	0.8	0.50
Salix scouleriana	0.3	0.50	0.5	0.71	0.5	0.71
Smilacina stellata	0.0	0.00	0.0	0.00	0.5	0.71
Spiraea betulifolia	1.5	1.57	3.0	2.37	1.7	1.86
Stipa occidentalis	0.5	0.71	0.0	0.00	0.0	0.00
Symphoricarpos albus	1.9	1.93	2.3	3.39	1.2	0.75
Taraxacum sp.	0.0	0.00	0.5	0.71	0.0	0.00
Thermopsis montana	3.2	2.21	8.2	2.86	8.7	3.67
Thalictrum occidentale	1.3	1.83	0.0	0.00	1.3	1.51
Trisetum canescens	0.6	1.00	1.5	2.74	3.2	2.48
Trifolium longipes	0.5	0.71	0.0	0.00	0.0	0.00
Trifolium plumosum	0.3	0.50	0.0	0.00	0.3	0.50
Trifolium repens	0.5	0.71	0.0	0.00	0.0	0.00
Urtica dioica	0.0	0.00	0.0	0.00	1.0	1.41
Vaccinium membranaceum	1.8	2.37	1.3	2.07	1.7	2.42
Vaccinium scoparium	3.6	3.23	8.3	5.28	9.2	7.36
Viola sp.	0.2	0.51	0.8	1.18	2.2	2.71

Appendix 4A Continued.

SPECIES	NO HERBIVORY $\bar{X}$	NO HERBIVORY SD	LOW DENSITY $\bar{X}$	LOW DENSITY SD	HIGH DENSITY $\bar{X}$	HIGH DENSITY SD
LOGGED FOREST						
Achillea millefolium	1.8	1.11	5.5	5.05	4.5	2.89
Agoseris sp	0.5	0.71	0.0	0.00	0.0	0.00
Amelanchier alnifolia	0.3	0.50	0.0	0.00	1.0	0.00
Antennaria luzuloides	0.4	0.70	0.5	0.58	0.2	0.41
Antennaria rosea	1.7	2.66	1.0	1.41	0.0	0.00
Aquilegia formosa	0.0	0.00	0.0	0.00	0.5	0.71
Arnica cordifolia	2.8	2.82	2.0	0.82	1.0	1.15
Arnica sororia	0.8	0.96	1.0	1.41	0.0	0.00
Arenaria macrophylla	0.3	0.50	0.5	0.58	0.0	0.00
Arctostaphylos uva-ursi	2.8	2.41	2.2	1.72	5.2	2.79
Aster conspicuus	0.3	0.50	0.0	0.00	1.0	1.41
Astragalus sp.	0.5	0.84	0.5	0.71	0.8	0.50
Berberis repens	0.9	0.83	0.5	1.00	0.8	0.96
Brodiaea douglasii	0.0	0.00	0.0	0.00	0.5	0.71
Bromus carinatus / inermis	1.9	0.99	4.2	3.19	1.8	2.87
Bromus mollis	0.0	0.00	0.5	0.71	0.0	0.00
Bromus tectorum	0.3	0.78	2.2	2.40	1.5	1.38
Carex geyeri	5.2	3.21	8.8	4.88	8.5	5.96
Carex hoodii	0.5	0.58	0.0	0.00	0.0	0.00
Calochortus sp.	0.7	0.82	0.0	0.00	0.0	0.00

Appendix 4A Continued.

SPECIES	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Carex rossii / concinnoides	0.7	1.06	2.0	2.10	5.5	2.65
Calamagrostis rubescens	6.6	4.10	13.7	10.48	10.7	3.33
Ceanothus velutinus	2.0	1.41	1.0	0.00	3.5	5.74
Chimaphila umbellata	1.5	2.12	0.0	0.00	0.0	0.00
Cirsium vulgare	0.2	0.41	0.0	0.00	2.0	1.83
Clarkia pulchella	0.0	0.00	0.5	0.71	0.0	0.00
Collomia sp.	0.5	0.58	0.0	0.00	0.8	0.96
Collinsia parviflora	0.8	1.16	0.8	0.96	0.3	0.50
Cryptantha affinis	0.0	0.00	0.0	0.00	0.5	0.71
Dactylis glomerata	0.8	1.47	1.5	1.22	3.8	4.26
Deschampsia elongata	0.0	0.00	0.0	0.00	0.5	0.71
Disporum trachycarpum	0.5	0.71	0.0	0.00	0.0	0.00
Dodecatheon sp.	0.0	0.00	0.0	0.00	0.5	0.71
Epilobium angustifolium	1.3	1.03	1.0	0.82	0.5	0.71
Epilobium paniculatum	2.3	2.94	2.2	2.56	0.0	0.00
Epilobium watsonii	1.0	1.41	0.0	0.00	3.5	4.95
Festuca idahoensis	0.0	0.00	1.0	1.41	3.5	0.71
Festuca occidentalis	1.1	1.29	1.8	3.25	2.3	1.71
Frasera speciosa	0.0	0.00	0.5	0.71	0.0	0.00
Fritillaria pudica	0.5	0.71	0.0	0.00	0.0	0.00
Fragaria vesca	2.7	1.83	7.3	4.68	3.7	3.20

Appendix 4A Continued.

SPECIES	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Fragaria virginiana	4.3	4.63	3.3	2.50	2.8	2.23
Galium triflorum	0.0	0.00	2.0	1.41	0.0	0.00
Geum triflorum	0.5	0.71	0.0	0.00	0.0	0.00
Grindelia nana	0.0	0.00	1.0	1.41	0.0	0.00
Heuchera cylindrica	0.0	0.00	0.0	0.00	0.5	0.71
Hieracium albiflorum	0.5	0.67	0.3	0.82	0.2	0.41
Hieracium albertinum	1.4	1.58	1.2	0.75	0.8	0.50
Koeleria cristata	0.3	0.50	0.5	0.71	1.5	2.12
Lactuca serriola	0.0	0.00	0.0	0.00	0.5	0.71
Linnaea borealis	1.1	1.45	0.7	1.21	0.8	0.50
Lithospermum ruderale	0.8	0.96	0.0	0.00	0.0	0.00
Lupinus caudatus	1.0	1.15	0.0	0.00	0.0	0.00
Lupinus sericeus	3.0	2.71	1.0	0.00	2.5	0.71
Lupinus sulphureus	0.0	0.00	0.0	0.00	0.5	0.71
Madia glomerata	0.0	0.00	0.0	0.00	0.5	0.55
Madia gracilis	1.0	1.41	0.0	0.00	0.0	0.00
Madia minima	0.3	0.71	0.7	0.52	1.5	0.71
Microseris nutans	0.5	0.71	0.0	0.00	0.0	0.00
Microsteris gracilis	0.7	1.03	1.0	1.15	2.0	2.83
Mitella stauropetala	0.7	0.82	0.5	0.71	0.3	0.50
Orthocarpus purpurascens	0.0	0.00	0.5	0.71	0.0	0.00

Appendix 4A Continued.

SPECIES	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Pachistima myrsinites	2.5	1.91	1.5	1.73	0.0	0.00
Penstemon confertus	0.5	0.71	0.0	0.00	0.0	0.00
Penstemon deustus	0.3	0.50	0.5	0.71	0.0	0.00
Penstemon glandulosus	0.3	0.50	0.5	0.71	0.0	0.00
Phlox sp.	0.8	1.60	0.5	0.71	1.5	2.38
Poa pratensis	0.1	0.35	1.0	0.00	0.7	0.82
Polemonium pulcherrimum	0.5	0.71	0.0	0.00	0.0	0.00
Potentilla glandulosa	1.0	1.15	0.3	0.50	0.2	0.41
Potentilla gracilis	1.0	1.41	0.0	0.00	0.0	0.00
Prunella vulgaris	0.5	0.58	0.0	0.00	0.0	0.00
Pyrola secunda	0.5	0.58	0.0	0.00	0.0	0.00
Ranunculus sp.	0.5	0.67	0.7	0.52	0.3	0.52
Ribes sp.	2.0	1.41	0.0	0.00	0.0	0.00
Rosa sp.	2.3	2.22	0.8	0.98	1.2	1.17
Rumex occidentalis	0.6	0.84	0.5	0.55	0.8	0.96
Salix scouleriana	0.3	0.50	1.0	0.00	0.0	0.00
Scutellaria angustifolia	0.0	0.00	0.5	0.71	0.0	0.00
Sedum stenopetalum	0.3	0.50	2.5	3.54	0.0	0.00
Sisyrinchium douglasii	0.0	0.00	0.0	0.00	0.5	0.71
Spiraea betulifolia	1.7	2.10	0.7	0.82	1.3	1.86
Stipa occidentalis	0.6	1.06	0.0	0.00	0.2	0.41

Appendix 4A Continued.

SPECIES	NO HERBIVORY $\bar{X}$	NO HERBIVORY SD	LOW DENSITY $\bar{X}$	LOW DENSITY SD	HIGH DENSITY $\bar{X}$	HIGH DENSITY SD
Symphoricarpos albus	2.2	2.21	2.3	1.03	0.8	1.17
Taraxacum sp.	0.0	0.00	0.5	0.58	0.0	0.00
Thermopsis montana	2.4	1.90	2.5	2.66	3.8	3.10
Tragopogon dubius	0.5	0.53	0.8	0.75	0.0	0.00
Trisetum canescens	0.7	1.06	0.8	0.98	1.3	1.89
Vaccinium membranaceum	0.5	0.71	0.5	0.71	0.0	0.00
Vaccinium scoparium	0.6	0.84	2.8	2.50	1.0	1.10
Viola sp.	0.7	1.07	1.5	2.39	0.7	0.82
Zigadenus venenosus	0.0	0.00	0.5	0.71	0.5	0.71
Unknown forbs	0.5	0.71	0.0	0.00	0.5	0.71
Unknown graminoids	0.0	0.00	2.5	3.54	0.0	0.00
GRASSLANDS						
Achillea millefolium	1.7	1.49	1.3	1.51	1.5	1.29
Agropyron spicatum	5.3	5.08	6.7	8.55	5.2	4.21
Aira sp.	6.1	9.26	8.0	11.31	12.0	11.69
Allium acuminatum	0.8	1.32	0.3	0.50	1.7	3.14
Antennaria luzuloides	0.9	1.13	1.0	1.27	0.0	0.00
Arnica sororia	0.0	0.00	1.0	1.41	0.0	0.00
Brodiaea douglasii	0.3	0.50	0.0	0.00	0.5	0.58
Bromus carinatus / inermis	0.5	0.71	0.0	0.00	0.0	0.00
Bromus mollis	0.5	1.22	0.0	0.00	3.2	3.12

Appendix 4A Continued.

SPECIES	NO HERBIVORY $\bar{X}$	NO HERBIVORY SD	LOW DENSITY $\bar{X}$	LOW DENSITY SD	HIGH DENSITY $\bar{X}$	HIGH DENSITY SD
Bromus tectorum	0.3	0.50	0.5	0.71	3.5	4.95
Carex geyeri	0.5	0.71	0.0	0.00	0.0	0.00
Camassia quamash	1.9	3.18	2.3	4.50	2.0	2.83
Calochortus sp.	0.0	0.00	1.0	1.41	0.0	0.00
Calamagrostis rubescens	0.0	0.00	0.5	0.71	0.0	0.00
Clarkia pulchella	0.5	0.58	0.0	0.00	1.5	1.91
Collomia sp.	1.3	2.42	0.0	0.00	1.5	1.73
Danthonia unispicata	4.8	3.13	2.7	1.37	5.0	2.68
Delphinium sp.	0.8	0.96	1.0	1.41	0.5	0.71
Dodecatheon sp.	0.0	0.00	1.0	1.41	0.0	0.00
Epilobium angustifolium	0.5	0.71	0.0	0.00	0.0	0.00
Epilobium paniculatum	0.0	0.00	0.5	0.58	2.0	2.83
Erigeron chrysopsidis	0.7	1.06	3.3	4.46	1.0	0.82
Eriogonum heracleoides	2.7	2.63	2.5	3.21	1.5	1.29
Festuca idahoensis	0.3	0.52	1.8	2.22	3.0	2.83
Festuca occidentalis	1.7	2.66	0.7	0.52	0.0	0.00
Fragaria virginiana	0.0	0.00	1.5	0.71	0.0	0.00
Geum triflorum	0.0	0.00	0.5	0.71	0.0	0.00
Geranium viscosissimum	1.5	2.12	0.0	0.00	0.0	0.00
Grindelia nana	0.9	1.73	2.0	2.16	1.3	1.26

Appendix 4A Continued.

SPECIES	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Koeleria cristata	2.3	2.58	0.8	0.96	0.0	0.00
Linanthus harknessii	0.0	0.00	1.0	1.41	0.0	0.00
Lomatium sp.	2.4	3.55	1.0	1.41	0.8	1.60
Lupinus sericeus	1.5	1.91	0.0	0.00	2.0	2.45
Lupinus sulphureus	0.0	0.00	0.0	0.00	1.0	1.41
Luzula campestris	0.3	0.52	0.0	0.00	0.5	0.58
Madia glomerata	0.0	0.00	1.0	1.41	2.0	2.83
Madia gracilis	0.0	0.00	0.0	0.00	0.5	0.58
Madia minima	0.8	2.04	0.8	0.50	1.5	2.12
Microseris nutans	1.0	1.41	0.0	0.00	0.5	0.71
Microsteris gracilis	0.0	0.00	0.5	0.71	0.0	0.00
Orthocarpus purpurascens	0.1	0.35	0.5	0.71	0.5	0.84
Phlox sp.	1.5	2.38	0.0	0.00	0.5	0.71
Poa sp.	1.3	2.50	1.0	1.41	1.0	1.41
Poa bulbosa	2.8	4.19	0.0	0.00	2.8	4.86
Poa pratensis	1.4	2.13	1.3	2.50	0.5	1.00
Polygonum douglasii	0.5	1.22	0.0	0.00	1.0	1.41
Potentilla glandulosa	0.0	0.00	1.0	1.41	0.0	0.00
Scutellaria angustifolia	1.3	0.96	1.0	1.15	0.0	0.00
Sedum stenopetalum	3.8	4.17	6.7	8.09	0.5	0.71
Sisyrinchium douglasii	0.5	0.71	0.0	0.00	0.0	0.00

Appendix 4A Continued.

SPECIES	NO HERBIVORY $\bar{X}$	NO HERBIVORY SD	LOW DENSITY $\bar{X}$	LOW DENSITY SD	HIGH DENSITY $\bar{X}$	HIGH DENSITY SD
Sitanion hystrix	0.5	0.71	0.0	0.00	0.0	0.00
Stipa occidentalis	0.5	0.71	0.5	0.71	0.0	0.00
Tragopogon dubius	0.5	0.71	0.0	0.00	0.0	0.00
Trisetum canescens	0.5	0.71	0.0	0.00	0.0	0.00
Trifolium plumosum	1.0	1.41	0.0	0.00	0.0	0.00
Trifolium repens	0.0	0.00	0.5	0.71	0.0	0.00
Unknown graminoids	1.0	1.41	0.0	0.00	0.0	0.00
XERIC FOREST						
Achillea millefolium	2.3	1.56	3.5	3.78	4.3	2.07
Agoseris grandiflora	0.0	0.00	0.5	0.71	0.0	0.00
Agropyron spicatum	2.2	2.21	2.3	1.37	4.7	5.32
Agrostis sp.	0.0	0.00	0.0	0.00	1.5	2.12
Aira sp.	0.0	0.00	0.5	0.71	1.5	1.29
Allium acuminatum	0.3	0.46	0.8	0.96	0.5	1.00
Amelanchier alnifolia	1.3	1.26	0.0	0.00	0.0	0.00
Antennaria luzuloides	0.6	0.74	0.5	0.58	0.3	0.50
Antennaria rosea	0.0	0.00	0.0	0.00	0.5	0.71
Arnica cordifolia	2.6	3.18	0.5	0.84	1.5	2.35
Arnica sororia	0.5	0.55	0.5	0.71	0.8	0.96
Arctostaphylos uva-ursi	3.5	1.73	1.5	0.71	2.5	0.71
Balsamorhiza sagittata	0.8	1.17	0.0	0.00	0.3	0.52

Appendix 4A Continued.

SPECIES	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Brodiaea douglasii	0.3	0.46	0.5	0.55	0.0	0.00
Bromus carinatus / inermis	0.8	1.17	0.5	0.71	0.8	0.50
Bromus mollis	0.2	0.41	1.0	0.00	2.3	1.26
Bromus tectorum	0.8	1.50	0.0	0.00	6.0	1.41
Carex geyeri	4.6	3.18	9.0	10.49	10.7	5.89
Carex rossii / concinnoides	1.3	1.89	0.3	0.50	0.0	0.00
Camassia quamash	0.5	1.22	1.5	2.38	1.0	1.41
Calochortus sp.	0.4	0.74	0.5	0.84	0.5	0.71
Calamagrostis rubescens	3.7	3.77	6.0	9.32	5.3	2.88
Collomia sp.	0.5	0.80	0.3	0.52	0.8	1.60
Dactylis glomerata	1.5	2.38	0.0	0.00	0.3	0.50
Danthonia unispicata	1.9	1.66	6.5	5.92	6.3	2.80
Delphinium sp.	0.4	0.52	0.0	0.00	0.5	0.58
Dodecatheon sp.	0.3	0.52	0.5	0.71	0.3	0.50
Epilobium paniculatum	0.2	0.41	0.0	0.00	0.5	0.55
Erigeron chrysopsidis	1.3	1.26	4.0	1.41	0.5	0.71
Eriogonum flavum	0.0	0.00	0.5	0.71	0.0	0.00
Eriogonum heracleoides	0.6	0.92	1.3	0.50	2.0	2.00
Festuca idahoensis	4.8	4.43	13.8	3.24	7.3	3.72
Festuca occidentalis	1.0	1.63	0.3	0.52	2.0	2.83
Fragaria vesca	0.5	0.76	2.5	1.00	0.0	0.00

Appendix 4A Continued.

SPECIES	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Fragaria virginiana	1.0	1.77	1.5	1.29	0.5	0.58
Fritillaria pudica	0.7	1.06	0.5	1.00	0.8	0.98
Galium triflorum	0.5	0.71	0.0	0.00	0.0	0.00
Geranium viscosissimum	0.5	0.71	0.0	0.00	0.0	0.00
Geum triflorum	0.8	0.96	0.5	0.71	0.0	0.00
Grindelia nana	1.8	1.90	3.3	3.56	2.3	2.07
Helianthus nuttallii	1.0	1.41	0.0	0.00	1.5	0.71
Hieracium albiflorum	0.0	0.00	0.5	0.71	0.5	0.71
Hieracium albertinum	3.3	3.50	3.5	2.12	1.0	0.82
Koeleria cristata	0.8	1.11	1.7	2.25	0.8	1.33
Lomatium sp.	0.5	0.55	0.0	0.00	0.5	0.71
Lupinus sericeus	3.8	3.49	5.8	4.99	2.5	3.02
Lupinus sulphureus	4.5	6.36	1.0	1.41	0.0	0.00
Luzula campestris	0.5	1.00	0.5	0.71	0.5	0.71
Madia glomerata	0.2	0.41	0.3	0.50	0.5	0.71
Madia gracilis	0.0	0.00	0.5	0.71	0.5	0.58
Madia minima	0.2	0.42	0.7	1.21	0.5	0.58
Microseris nutans	1.0	0.89	0.3	0.50	0.5	0.71
Microsteris gracilis	0.0	0.00	0.5	0.71	0.0	0.00
Montia perfoliata	0.0	0.00	0.0	0.00	0.5	0.71
Naverretia sp.	0.5	0.71	0.5	0.71	0.0	0.00

Appendix 4A Continued.

SPECIES	NO HERBIVORY $\bar{X}$	NO HERBIVORY SD	LOW DENSITY $\bar{X}$	LOW DENSITY SD	HIGH DENSITY $\bar{X}$	HIGH DENSITY SD
Orthocarpus purpurascens	0.2	0.41	2.0	2.83	0.5	0.58
Phleum pratense	0.5	0.84	0.0	0.00	0.3	0.52
Phlox sp.	0.0	0.00	0.5	0.71	0.0	0.00
Poa sp.	0.0	0.00	0.5	0.71	0.0	0.00
Poa pratensis	1.0	1.59	2.3	3.01	2.7	1.97
Polygonum douglasii	0.0	0.00	0.0	0.00	0.5	0.71
Potentilla glandulosa	0.0	0.00	0.5	0.71	0.0	0.00
Rosa sp.	0.5	0.58	0.5	0.71	0.0	0.00
Rumex occidentalis	0.5	0.58	0.0	0.00	0.5	0.71
Scutellaria angustifolia	0.3	0.50	0.0	0.00	0.3	0.50
Sedum stenopetalum	5.6	4.48	7.3	10.50	4.5	3.99
Senecio sp.	1.0	1.05	0.3	0.52	0.0	0.00
Sidalcea oregana	0.5	0.71	0.0	0.00	0.0	0.00
Sisyrinchium douglasii	0.0	0.00	0.8	0.96	0.0	0.00
Sitanion hystrix	0.0	0.00	1.0	1.41	0.0	0.00
Spiraea betulifolia	1.3	0.82	0.5	0.71	0.3	0.50
Stipa occidentalis	0.0	0.00	0.0	0.00	0.5	0.58
Symphoricarpos albus	1.5	1.38	4.3	5.68	1.8	1.26
Taraxacum sp.	0.3	0.50	0.0	0.00	0.0	0.00
Tragopogon dubius	0.5	0.71	0.0	0.00	0.0	0.00
Trisetum canescens	0.3	0.50	0.0	0.00	2.5	3.54

Appendix 4A Continued.

SPECIES	NO HERBIVORY		LOW DENSITY		HIGH DENSITY	
	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Trifolium longipes	3.0	0.0	0.0	0.00	1.0	1.41
Trifolium plumosum	0.5	0.71	0.0	0.00	1.5	0.71
Trifolium repens	0.0	0.00	0.0	0.00	1.0	1.41
Zigadenus venenosus	0.5	0.85	1.5	1.87	1.0	1.41

CONCLUSIONS

Interactions among niche partitioning by ungulates and plant production with density-dependent processes are indeed the key to understanding the role that large herbivores play in ecosystem structure and function. Understanding of density-dependent responses by animals to changing availability of resources and how those processes interact with plant communities improve our understanding of niche relationships among species of large, herbivorous mammals. Niche separation is traditionally evaluated along spatial, temporal, and dietary axes, and conclusions about niche dynamics from a single niche axis alone may lead to misinterpretation of results.

My analyses of niche relationships among Rocky Mountain elk, Rocky Mountain mule deer, and cattle indicated resource partitioning in use of space, habitats and diets. Those species differed in use of space, especially elevation, steepness of slope, and use of logged forests. Examination of diets indicated strong partitioning of dietary niche and some separation of habitats that was related to moisture regimes, mule deer used more xeric habitats than either elk or cattle. Contrary to predictions, mule deer had the greatest variability in diets, and foraged on more xeric forages than did either elk or cattle.

When I used 2 temporal windows to examine both immediate (6 h) and long term (7 days) effects of competition I observed strong avoidance over a 6-h period among those 3 ungulates. That effect was weaker for the previous 7 days. Thus, cattle were generalists with respect to habitat selection; the 2 native herbivores avoided areas used by cattle. Mule deer and elk avoided one another during the short temporal window (6 h), although spatial differences in habitat use often were not maintained over 7 days. I

examined changes in habitat use by mule deer and elk following addition of cattle in spring and removal of cattle in autumn and demonstrated that both elk and mule deer changed use of habitats in response to cattle presence, indicating competitive displacement.

The manipulative experiment of population density indicated that density-dependent feedbacks affected physical condition and reproduction of adult female elk. Elk that were in poor physical condition were less likely to reproduce, particularly if they had recruited an offspring the previous year. Age-specific pregnancy rates were lower in the high-density area, although there were no differences in pregnancy of yearlings or age at peak reproduction between areas. Age-specific rates of pregnancy began to diverge at 2 years of age between the two populations and peaked at 6 years old. Pregnancy rates were most affected by body condition and mass, although successful reproduction the previous year also reduced pregnancy rates during the current year. Our results indicated that while holding effects of winter constant, population density and density-dependent mechanisms had a much greater effect on physical condition and fecundity than density-independent factors (e.g., precipitation and temperature).

I examined interactions of population density of elk and plant productivity. Net aboveground primary productivity (NAPP) increased from no herbivory to moderate grazing intensity and then declined as grazing intensity continued to increase. Apparent offtake followed a similar pattern and was greatest at intermediate levels of grazing intensity and then declined as herbivores and NAPP approached zero. I observed no

changes in species composition with our density manipulations, probably because of the extensive history of grazing by native and domestic herbivores. Those data indicated that increases in NAPP at low to moderate levels of herbivory occurred in montane ecosystems. Compensatory responses by plants are more difficult to detect when responses to herbivory are subtle and occur at relatively low grazing intensity. This experimental approach combined with an independent measure of grazing intensity to directly evaluate the presence of herbivores allowed detection of those processes. My examination of grazing intensity on NAPP indicated that in many ecosystems, positive responses to grazing intensity likely occur at low levels of herbivory, or low population density with respect to ecological carrying capacity (K).

I observed strong effects of density dependent processes on physical condition of individual elk and reductions in NAPP of plant communities with high levels of grazing intensity. At high population densities, resources for elk declined because plant communities were unable to sustain those high levels of grazing and NAPP was substantially reduced. At low population density of large herbivores and moderate levels of grazing intensity NAPP was increased, likely indicating compensatory responses by plants, and elk were in good physical condition and exhibited high rates of reproduction. Life-history strategies of large herbivores cause density-dependent feedbacks that help regulate population dynamics and those same processes have substantial effects on ecosystem functioning.

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